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Changes in Distribution and Habitat Associations of Wolffish (Anarhichidae) in the Grand Banks and Labrador Shelf

Changements dans la répartition des loups de mer (Anarhichidae) et l'habitat fréquenté sur les Grands Bancs et le plateau continental du Labrador

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Abstract

The *Species at Risk Act* (SARA) recognizes habitat for species designated at risk as an important component for their survival and recovery. In this study, we review the available information on habitat requirements for three species of wolffish in the western Atlantic. Specifically, the life history and ecology of wolffish are reviewed, their current and historic distributions are described and distributions are modeled in relation to available habitat information. The results are interpreted in relation to critical habitat requirements of the *Species at Risk Act*. The three wolffish species are at the center of their distribution, reaching highest density and covering the largest area on the northeast Newfoundland and Labrador Shelf. There they distribute over a wide range of depths, from about 25 m to > 1 400 m., *A. denticulatus* occupying the widest range, *A. lupus* the narrowest. We show that temperature is an important feature of wolffish habitat. All three species are associated with a narrow thermal range of above average bottom temperatures, mainly 1.5-4.5^{0}C, absent where temperatures are < 0^{0}C. Based on the results of this study, wolffish may be classified as "temperature keepers" – they maintain a similar temperature range by changing their distribution, in this case a reduction, co-occurring with a period of reduced abundance. The distribution of wolffish is also related to sediment type. Analysis of bottom type data using ROXANN data indicated that *A. minor* and *A. lupus* were widely distributed on various sediment types. *A. denticulatus*, however, did occupy sand/shell hash, gravely sand and rock sediments more frequently. *A. lupus* in near-shore areas avoided sediments that can be stirred up such as muddy substrates. The area where wolffish were concentrated corresponds to the most heavily fished grounds along the outer shelf. The rate of decline at the unfished locations was observed to be similar or higher than in the most intensely fished areas. Thus, there is no evidence of cropping down by the fisheries. However, changes in ambient temperature resulted in a greater proportion of the wolffish being concentrated on the outer shelf where fishing intensity was greatest, thus making them more vulnerable to capture.

Résumé

Il est reconnu dans la *Loi sur les espèces en péril* (LEP) que l'habitat des espèces en péril est important pour leur survie et leur rétablissement. Nous faisons ici un bilan des renseignements disponibles sur les besoins en matière d'habitat de trois espèces de loup de l'Atlantique Ouest : nous passons en revue leur cycle vital et leur écologie, nous décrivons leur répartition actuelle et historique et nous modélisons leur répartition en regard des données disponibles sur leur habitat. Puis nous interprétons les résultats en fonction des besoins essentiels en matière d'habitat établis dans la LEP. Les trois espèces de loup sont retrouvées au centre de leur aire de répartition, atteignant la densité la plus élevée et fréquentant la superficie la plus grande sur le plateau continental du Labrador/nord-est de Terre-Neuve. Elles y sont retrouvées à une vaste gamme de profondeurs, soit d'environ 25 m à plus de 1 400 m, *A. denticulatus* fréquentant la plus vaste gamme de profondeurs et *A. lupus* la plus faible. Nous montrons que la température est un élément important de l'habitat du loup. Les trois espèces favorisent une plage étroite de températures au fond supérieures à la moyenne, se situant entre 1,5 à 4,5 ^{0}C, mais évitent les eaux de moins de 0 ^{0}C. D'après les résultats de cette étude, les loups peuvent être classés comme des « disciples de la température » – ils se déplacent de sorte à rester dans des eaux de température semblable, ce qui mène à un changement dans leur aire de répartition, dans ce cas en la réduisant, et à une abondance réduite. La répartition des loups est fonction aussi du type de sédiment. Une analyse des données ROXANN sur les types de fond a révélé que *A. minor* et *A. lupus* sont distribués à grande échelle sur divers types de fond, alors que *A. denticulatus* préfère des fonds composés d'un mélange de sable et de coquillage, des fonds de sable graveleux et des fonds rocheux. Près des côtes, *A. lupus* évite les endroits recouverts de sédiments pouvant être déplacés, comme les fonds boueux. Les eaux où les loups étaient concentrés correspondent aux lieux de pêche les plus fortement exploités le long de la plate-forme extérieure. Le taux de déclin aux endroits non exploités est semblable à ce qu'il est aux endroits les plus exploités et même plus élevé; il n'y a donc pas d'indication que les pêches sont à l'origine de la réduction des effectifs. Par contre, les changements dans la température ambiante ont mené à la concentration d'une plus grande proportion des loups de mer dans les eaux de la plate-forme extérieure où l'intensité de pêche est la plus forte, ce qui les rend davantage vulnérable à la capture.

Introduction

Three species of Family Anarhichadidae: *Anarhichas minor* (spotted wolffish), *A. denticulatus*, (northern or broadhead wolffish) and *A. lupus*, (Atlantic or striped wolffish) inhabit the North Atlantic. In the northeast Atlantic, all three species are distributed from Iceland to the Barents Sea (Barsukov 1959, Baranenkova et al. 1960) and off southern Greenland, (Möller and Rätz 1999, Stransky 2001), the latter contiguous with Canadian waters. Their distribution in the northwest Atlantic extends from Davis Strait and northern Labrador to the southern Grand Banks and Flemish Cap (Albikovskaya, L.K. 1982, Kulka and DeBlois 1996, Fig. 1). McRuer et *al.* (2001) noted that *A. lupus* was also common in the deeper parts of the Gulf of St. Lawrence, on the Scotian Shelf, in the Gulf of Maine and in the Bay of Fundy. The other two species are only occasionally observed in these areas. All three species extend into USA waters, but there they are uncommon (*A. lupus*) or rare (*A. minor* and *A. denticulatus)* (Musick, 1999).

Information pertaining to population structure, distribution, habitat association or life history of any of the wolffish species is limited. As yet, their stock structure has not been defined and most of the current knowledge on distribution and biology for the northwest Atlantic is derived from papers published by Templeman in the 1980s (Templeman 1984, 1985 1986a, 1986b). More recent work on population trends and distribution include McRuer et *al.* (2001) on the Scotian Shelf and Gulf of St. Lawrence and Simpson and Kulka (2002) on the Grand Banks, northeast Newfoundland and Labrador Shelves. A summary is provided below.

Biology

Musick (1999) classified wolffish as "low" productivity species, based on growth, fecundity and age characteristics of *A. lupus* in USA waters. The testes of these species are relatively small, sperm and egg production is low, fertilization is internal and eggs and larvae are large.

Although fecundity is low, internal fertilization (Pavlov 1994), nesting habits and egg guarding behaviour at least for *A. lupus* (Keats et al. 1985) effectively increases potential for survival of individuals during the early life stages. Spawning for *A. lupus* is known to occur in both shallow (5-15 m) inshore and deep offshore areas in September in Newfoundland waters. The entire larval stage is spent close to the hatching location (Templeman 1985 and 1986a). On individual scales, it appears that *A. lupus* requires areas of rock and boulder in which to deposit egg masses (Barsukov, 1959, Keats et *al* 1985). Egg clusters of A. *lupus* were also observed in offshore trawl catches from the Scotian Shelf (Powles 1967) but it is unknown whether egg guarding in crevices also occurs offshore. Characteristics of the spawning sites of *A. denticulatus* and *A. minor* is unknown, but they appear to spawn in late fall or early winter (Templeman 1985 and 1986a).

Wiseman (1997) reported that newly hatched larvae of *A. lupus* are quite large, about 2 cm. Recently hatched larvae remain on or close to the bottom. Following hatch and yolk sac absorption, wolffish larvae become pelagic where as a typical member of the plankton, large-scale patterns of temperature and salinity can potentially influence survivorship and subsequent recruitment into the adult population. *A. minor* also produces large eggs in clusters on the bottom and their pelagic larvae are found over the continental slopes (Templeman 1986a).While not directly applicable to *A. denticulatus*, limited investigations of the other two species does provide some insights of life history for this closely related species in the northwest Atlantic.

Habitat

Wolffish are demersal with only the young of the year inhabiting the upper water column, with the possible exception of *A. denticulatus* that may spend considerable time in the water column (Shevelev and Kuzmichev 1990, Templeman 1984). The three species are found in a wide range

of depths from near shore to about 1 200 m, but occur most often at depths > 100 m and inhabit a diverse range of bottom types in the northwest Atlantic (Simpson and Kulka 2002 and Kulka and Simpson 2004) *A. lupus* have been observed in crevices and under large rocks near shore within SCUBA diving range (Keats et *al.* 1985). The other two species, *A. minor* and *A. denticulatus* are rarely taken in survey trawls or fishing gear at depths < 100 m. Their association with bottom types is less well understood as they occur outside the range where they can be directly observed. However, Templeman (1986a) noted that *A. minor* inhabits offshore areas and diet suggests proximity to sand or mud bottoms. Unlike other wolffish, *A. denticulatus* has been observed off bottom during both juvenile and adult stages in the northeast Atlantic (Shevelev and Kuzmichev 1990).

Large scale habitat components affecting post-yolk sac absorption larval stages of wolffish include the influence of near surface circulation patterns. The East and West Greenland currents and the Irminger current, following mixing in the Davis Strait, are transported onto the Labrador Shelf and ultimately onto the Grand Bank (Drinkwater 1996). The cold West Greenland current emerging from the Davis Strait flows over the inner portion of the shelf, pooling on the northern Grand Bank. The warmer Irminger and East Greenland currents flow along the outer shelf. As well, the intensity of the Icelandic Low and Bermuda-Azores High influence the ice extent and affects the oceanic temperature distribution along the coast of Newfoundland and Labrador. Thus, large scale variation in annual, interannual and decadal temperature and salinity variation could potentially influence recruitment and survival in wolffish. Consequently, critical habitat would include sufficient areas in which the thermal and salinity preferences of wolffish (which are relatively unknown) are satisfied on longer (decadal) time scales. Comprehensive analysis of optimal conditions for each life stage of wolffish and large-scale modeling (temporal/spatial) of oceanic thermal/salinity conditions are required to define suitable or critical habitat on these scales.

On more regional scales, these areas should include, as part of the wolffish habitat, the near surface waters over much of the Northeast Newfoundland and Labrador Shelf where young of the year wolffish are widely distributed, as indicated by capture in IYGPT trawl surveys conducted in August and September, 1996-1999 (Simpson and Kulka 2002). Furthermore, small (<55 cm) *A. minor* and *A. lupus*, captured in fall trawl surveys, are found to be distributed in similar offshore areas (Simpson and Kulka 2002). These regional scale areas could also be considered critical for recovery and survival of wolffish populations.

For juvenile and adult stages, little is known about the associations relative to local sediment and bottom oceanic conditions. Such information would be required to determine the suitable habitat associations.

Rationale

The three species of wolffish have been designated at risk by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) based mainly on a population declines over the last two decades (indices derived from NL research surveys, summarized by Simpson and Kulka, 2002). Consequently they were listed on Sched. 1 of the *Species at Risk Act* (SARA) as: *A. minor*, and *A. denticulatus* - "threatened" and *A. lupus*, - "special concern".

Under SARA, the Government of Canada is obligated to conserve biological diversity through specific actions aimed at ensuring the survival of species listed under Sched. 1, designated as at risk of extinction (Kulka 2004). A key action that is considered important to the survival of a species designated as at risk of extinction constitutes the preservation of critical habitat. Sect. 41 and 49 of the Act specifies that such habitat, where possible, must be identified in recovery strategies or action plans. Examples of critical habitats may include but are not exclusive to

breeding sites, nursery areas or feeding grounds. Further, Sect. 58 of the Act specifies that it is illegal to destroy the critical habitat of a species at risk.

The Terms of Reference (TOR) for this series of papers, leading to the definition of critical habitat of fish, covered four main areas: Distribution review (past and present), Population Viability Analysis (PVA), Habitat Supply Modeling (HSP) and Spatial Mapping.

The study focuses on the center of distribution of the species, namely, the Grand Banks, northeast Newfoundland and Labrador Shelf (Fig. 1). The Arctic, Gulf of St. Lawrence, Scotian Shelf and Bay of Fundy constitute the fringe of the distribution of the species and are not part of this analysis. We approach the problem by employing spatial mapping and spatial statistics to describe distribution and habitat associations. We examine the relationship between survey catches of wolffish and available environmental factors: depth, temperature and sediment type, information gathered concurrently with catch data, with the purpose of determining habitat associations and to the extent possible, critical habitat for wolffish. Bottom temperature was deemed of particular interest given that Colbourne et al (2004) reported an extended cold period lasting from the mid-1980s to the mid-1990s and a fresher-than-normal period that lasted most of the decade of the 1990s, a period concurrent with the decline of wolffish species abundance reported by Simpson and Kulka (2002).

As well, this study examines local scale information, specifically *A. lupus* habitat preferences and behaviour as gathered through direct observation by divers in near-shore areas, a small fraction of the area occupied by the species. These direct observations are available only for *A. lupus* since the other two species distribute at depths greater than can be accessed by divers.

Finally, we compare changes in distribution of the wolffish within heavily to lightly fished and unfished locations to examine human effects. All three species are commonly taken as bycatch in a wide range of fisheries (Simpson and Kulka 2002) and therefore cropping down due to fishing mortality could explain or contribute to the changes in distribution and abundance observed.

Methods

Survey

Data on demersal species have routinely been collected during DFO NL (Fisheries and Oceans, Newfoundland and Labrador Region) trawl surveys, mainly during spring and fall on the Labrador Shelf northeast Newfoundland Shelf and the Grand Banks from 1971-2003 (Lat. 43^{0} to Lat. 58^{0}, Fig. 1). A total of 38,635 sets from all months of the year were used for this study.

Survey coverage was somewhat uneven over space and time (Table 1). Two seasonal surveys, in the spring and the autumn contributed to the data used for these analyses. Table 1 enumerates number of sets by year by month and by year groups and areas used in this study. Data from all months of the year were combined to yield annually averaged distributions. This pooling of data is reasonable as there is no evidence of extensive migration (Templeman, 1984) and maps of spring and autumn distributions, where they overlap showed very similar patterns. Analyses with respect to depth and temperature were done on a seasonal basis.

Doubleday (1981) summarizes the stratified random design adopted by DFO NL after 1971 for spring surveys, and after 1976 for fall surveys. Spring surveys of the Grand Banks (NAFO Divisions 3LNO) commenced in 1971 with the inclusion of Subdivision 3Ps (comprising St. Pierre Bank) since 1972. Autumn surveys of the northern Grand Bank (NAFO Division 3L) began in 1981, and then commenced for the southern Grand Bank (Divisions 3NO) in 1990. The St. Pierre Bank (southwest part of the study area) was not surveyed in the fall. While the survey design has remained constant over time, both inshore and deepwater strata have been added to the survey area in recent years (beginning in 1993), along with modifications to some of the original

strata. A summary of early modifications is in Bishop (1994) and a table summarizing depths fished and other survey parameters can be found in Kulka et *al* (2004).

In addition, there was a change in survey gear after the spring 1995 survey from an Engels 145 groundfish trawl to a Campelen 1800 shrimp trawl. Although both are bottom trawls, configuration and mesh size differ significantly, as described by Bishop (1994). Size and age based conversion factors for amounts and sizes of fish caught were derived for major commercial species, but not for wolffish species. Thus, catch rate data (weight and number per tow) are on a different scale starting in of autumn 1995. This gear change affected selectivity by fish size for major commercial species and this could also be the case for wolffish species. For the purpose of mapping abundance (numbers per standard survey tow), a conversion factor was derived from the knife-edge change in abundance over the time of the gear change, based on an average of the 1996 and 1997 set abundance estimates divided by an average of the same estimates for 1994-1995, the years that straddle the survey gear changeover. This conversion factor was then applied to survey numbers per tow to "Campelenize" values prior to 1995, and thus provides continuity of scale, with the caveat that it does not account for size base differences, over the full time series.

Extra survey sets that were not part of standard surveys have been added where available. Although these sets are a deviation from the proportional allocation of sets when used to estimate biomass using the STRAP (Stratified Random Program) model (Smith and Somerton 1981) they use the same sampling protocol as standard survey sets. Their addition for this analysis does not violate allocation of sets within a stratified model since the Geographical Information System (GIS) used for spatial analysis does not make use of pre-defined strata used by STRAP. These extra sets serve to enhance the spatial coverage and thus are included in the present mapping of wolffish and bottom temperature distributions.

The survey dataset comprises geo-referenced estimates of weight and number per tow for each species plus depth and temperature readings. These data were grouped into five multi-year components based on wolffish population trends. Simpson and Kulka (2002) showed that abundance fluctuated similarly for all three species. Four periods were chosen for the analysis corresponding to observed changes in abundance. The period 1971-1977 (Pre), predated the period in which the three species reached a maximum population size. These sets constitute the earliest available survey data. This period was relatively poorly sampled (areas missed) and subsequent analyses should be regarded with caution. The period 1978-1984 (High) corresponded to peak abundance, 1985-1989 (Decline) was a period of decline, abundance was at its lowest during 1990-1995 (Low) and 1995-2003 (Current) is the current period. The latter period also corresponds to when the Campelen trawl was employed and thus changes in patterns in that period may in part be a result of change in survey gear.

As yet, stock structure has not been defined for the wolfish species. Within our area of study, there are no apparent discontinuities in the distribution of adults or young. However, the study region was divided into 4 sub-areas: Norlab – Labrador Shelf, the area north of Lat. 55^0 30'; Lab – Labrador Shelf north of Lat. 55^0 30' and south of Lat. 55^0 30'; GB – Grand Banks; Laur – Laurentian Channel, west of Lon. 56^0 (refer to Fig. 1). These areas were selected based on observed differences in distribution, environmental conditions and in abundance trends (refer to Simpson an Kulka 2002 for abundance differences by area). Norlab and Lab underwent similar abundance trends but the two areas were created because the survey was sporadic north of Lat. 55^0 30'. The area GB was treated separately from Lab to the north because of the very different pattern of distribution between the two areas. *A. denticulatus* and *A. minor* were widely distributed across the entire shelf area within Lab and NorLab but occurred only along the shelf edge in GB and Laur. Bottom topography also differed between these areas, Lab and NorLab constituted a series of deep banks separated by very deep channels whereas GB constituted a large, flat and shallow series of banks surrounded by steep slope waters where the large majority

of wolffish inhabited. The exception was *A. lupus* which occupied the flat, shallow part of the southern extent of the Grand Bank. Laur comprised a deep trench leading into the Gulf of St Lawrence where bottom temperatures were consistently warmer than other areas.

Finally, the bottom temperature analyses used two periods within the year: Warming – June-Nov. and Cooling – Dec-May to differentiate seasonal differences.

Distribution

Patterns of distributions and measures of area occupied were examined to provide insight into habitat associations. The annual surveys were designed primarily to enumerate over a broad area, major commercial species such as Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*) and Greenland halibut (*Reinhardtius hippoglossoides*), and thus do not encompass the entire range of the wolffish species to the north. However, they do cover all areas where wolffish are concentrated and covers nearly the full depth range of the species except near shore (< 25 m).

Given that survey sets average about 20 km between locations within a given year, they may not capture information at the scale of residence of wolffish. Also, there is inter-annual variation in manner in which the surveys are conducted, which adds some uncertainty to the results. However, the data were sufficient to describe spatial variation and relation to recorded environmental variables.

Potential mapping in SPANS GIS (Anon. 2003) was used to investigate changes in the spatial distribution of wolffish and habitat associations using the geo-referenced survey data. This technique transforms point data Z values (survey fishing set abundance estimates and bottom temperature values) to a continuous surface that describe distribution, by placing a circle around each point and assigning the average value of that point plus all other points that fall within the circle, to the area of the circle. Where circles overlap, the values of the overlap areas are averaged. This process is performed on all of the points and effectively creates a very large number of crescents or circle fragments. The value of the crescents are assigned to an underlying grid and classified to yield 15 equal areas representing Z values. Details of this transformation including appropriate selection of parameter values and circle size are described in Kulka and Pitcher (2001).

The resulting maps define areas of similar values; in the case of distributions, it maps density categories as survey kg per tow and in the case of bottom temperature, it spatially categorizes temperature ranges. Darkest (red) areas represent highest densities of wolffish (highest numbers per tow), to blue, representing the lowest catch rate. Grey depicts sampled areas but with no wolffish present. White depicts un-sampled areas. A map was produced for each species for each time period described above.

Area of occupancy for the wolffish species was calculated within the GIS as the area (km^2) of the potential map surface within each density category. Temperature surfaces were created corresponding to warming and cooling periods described above.

Habitat Associations

We investigated the distribution of wolffish in relation to their association to three environmental variables; sediment type, ambient temperature and depth. Wolffish abundance in relation to bottom temperature and depth were derived by overlaying the points (sets) on the depth and temperature potential maps and calculating average abundance for each of fifteen depth or temperature categories.

In addition to potential mapping, the distribution of wolffish in representative years was modeled using a nonparametric Generalized additive models (GAM) in S-Plus (Math-Soft Inc. Seattle Washington) to analyse the catch in numbers in relation to location and environmental parameters. GAM models with a Poisson error distribution can quantify associations between spatial trends in wolffish catch and environmental factors (Swartzman et al. 1992, O'Brien and Rago 1996). We used a step-wise GAM to determine the best fitting model based on the Akaike Information Criterion (AIC) test statistic, where the lowest AIC gave the best combination of parameters for the final model. The model that returned the lowest AIC included terms to model wolffish catch as a function of depth, temperature, latitude and longitude in the form:

Catch number ~ s(depth) +s(temperature) + latitude + longitude

where s is the cubic spline smoothing function which models the shape of the response variable as a function of the predictor. GAM models were fit for representative years of wolffish abundance and pseudo-coefficient of determination (Pseudo-R squared) values were compared between full and partial models (excluding latitude and longitude). Pseudo-R squared values were calculated as the ratio of the model deviance to the null deviance (Swartzman et al 1992)

As well, we investigated the distribution of wolffish in relation to sediment type, temperature and depth through assessment of cumulative distribution functions. Seabed classification data (ROXANN), which have been collected since 1992 were used to relate sediment type in the vicinity of survey trawl locations. From these acoustic data, seabed *roughness* and *hardness* indices were derived to classify the sediment to categories of mud, sand, sand & shell, shell & pebbles, small rock, hard bottom, or undefined (Naidu and Seward 2002 unpubl. data). An average sediment type was calculated for each tenth of a degree of latitude and longitude and was used to classify survey trawl locations within each area by sediment type.

We initially compared the mean number of wolffish captured by sediment type on an annual basis. In addition, we compared the empirical distribution of sediment types present for all survey sets and the cumulative distribution function for only those sets in which wolffish were captured. Significant differences in available and occupied environments were tested using the Kolmogorov-Smirnov test of significance on the cumulative frequency distributions of the environmental variables. A similar comparison of cumulative distribution functions for temperature and depth, derived from the research trawl surveys were also conducted.

On a finer scale, the distribution of *A. lupus*, which distribute close to shore, was investigated at two inshore locations, Bonne Bay on the west coast of Newfoundland (7 sites) and Avalon Peninsula on the east coast (2 sites) through SCUBA surveys. At each site, dive transects were completed between the intertidal zone and 30 m. Wolffish were counted and the characteristics of the microhabitat in which they were observed was recorded. Dive data has been accumulated from dives between 1979 and 2004.

Results

Distribution

During 5 time periods examined, 1971-1977 (Pre), 1978-1984 (High), 1985-1989 (Decline) 1990-1995 (Low) and 1995-2003 (Current), survey catch rates on the northeast Newfoundland and Labrador Shelf were 3-40, 2-73 times and 1-6 times higher for *A. denticulatus*, *A. minor* and *A. lupus* respectively compared to the Grand Banks and the Laurentian Channel (Fig.2). The highest densities and greatest extent, and thus the center of distribution of the wolffish species occur on

the northeast Newfoundland and Labrador shelf, from Lat. 47 to 58°, particularly over the southern extent of that shelf (Fig. 3).

The distributions of the three wolffish species have undergone significant change since the commencement of standard surveys in 1971 (Fig. 3). The Pre period is not included in the following elaboration of results because the area surveyed during that time was substantially smaller, missing, all areas north of Lat. 55° 30'. However, during that period, for comparable areas surveyed, the three species occupied less area than during 1978-1984 (High).

A. denticulatus occupies the largest area of the three species. During the High period, 43% of the survey area, mainly on the shallow part of the Grand Banks and northeast of the island of Newfoundland contained no *A. denticulatus* (57% of the area occupied, Fig. 3 and 4, Table 2). In subsequent periods, area occupied as a percent of area surveyed contracted to 39.1% during the Decline (1995-1989) and to 19.4 % during the Low period (1990-spring 1995). Area occupied increased slightly to 23.4% during the Current period, since the fall of 1995.

Starting with the Decline, the area occupied decreased and became somewhat fragmented (Fig. 3a). The area previously occupied but now without *A. denticulatus* corresponds mainly to the inner part of the northeast Newfoundland and Labrador Shelf (Fig 3a, Current). The remaining fish were distributed along the shelf edge over the entire range, most highly concentrated between Lat. 47° and 51°.

The distribution of *A. minor* was quite similar to what was observed for *A. denticulatus* except that they seldom occurred in the deepest trenches, or as deep along the slope. During the High period, *A. minor* was densely concentrated from Lat. 59° to the northern Grand Bank. The extent of the distribution of this species also decreased during the Decline, finally concentrating on the outer shelf. During the Current period, this species has repopulated portions of the inner shelf. Area occupied changes were less variable than for *A. denticulatus*: ranging from High - 48.3% to Decline - 37.1% to Low - 22.5% Current - to 31.1% (Fig. 4, Table 2).

A. lupus underwent the most significant changes in the northern part of surveyed range, on the northeast Newfoundland and Labrador Shelf, similar to the other two species. Over the entire surveyed range, area occupied was: High – 55.0%, Decline – 47.4%, Low – 37.9%, Current – 56.4% (Fig. 3 and 4, Table 2). In contrast, a concentration of this species on the shallower part of the Grand Banks underwent relatively little change. Unlike areas to the north, the extent of this concentration has actually increased. On the Grand Banks, area occupied was: High - 47.8%, Decline - 53.5%, Low - 48.8%, Current - 77.0% (Fig. 3 and 4, Table 2).

In addition to area occupied, the degree of concentration changed over time for the three species. The area of highest concentration as a percent of total area surveyed decreased for all species (black portion of the lower graphs in Fig. 4). Over their entire range, all three species underwent a similar reduction in concentration: *A. denticulatus* - 65.2% to 0%, (percent of the occupied area contained high concentrations of fish, High period to Current period); *A. minor* - 72.6% to 4.3% and *A. lupus* - 56.2% to 3.8%. Although these three species occupy a larger area currently compared to the previous period, they are more dispersed. For *A lupus*, the reduction in concentration was less on the Grand Banks than the area to the north although in that area it too became more dispersed (Fig. 4b).

For this study, potential habitat is defined as the area where wolffish occurred during their maximum extent minus their current area occupied. This presently unoccupied area primarily corresponds to the inner portion of the northeast Newfoundland and Labrador Shelf for all three species (Fig. 5). However, the proportion presently unoccupied varies by species: 60% of 385 340 km^2, the maximum extent of *A. denticulatus*, 40% of 346 183 km^2 for *A. minor* and 13% of 438 499 km^2 for *A. lupus* (Table 3).

A mapping of centroids (geographical centers of high concentrations of wolffish) indicate that the most dense concentrations of *A. denticulatus* shifted southward from north of Lat. 54° during the period of decline and remained there during the Low and Current period (Fig. 6). A similar shift was less apparent for the other two species. However, high concentrations were observed during the Current period only to the south, centered at Lat. 48° 30' Lon. 51° just north of the Grand Banks. This constituted an area of persistently high concentrations for all three species during all periods surveyed (1971-2003).

Habitat Associations

The three species distribute over a wide range of depths. *A. denticulatus* was most widely distributed, taken in survey sets between 38 and 1 504 m (the maximum depth surveyed). *A. minor* and *A. lupus* were slightly more narrowly distributed across depths: 56-1 046 m and 25 (minimum depth surveyed) to 918 m respectively. Diving observations (elaborated later in the Results) show that *A. lupus* commonly occurred in waters shallower than 25 m. During Dec-May, densest concentrations of *A. denticulatus* occurred between 500 and 1 000 m with some shift to shallower depths in Jun-Nov (Fig. 7). Densest concentrations of *A. minor* occurred between 200 and 750 m at all times of the year, peaking in shallower waters (300 m) in Jun-Nov. *A. lupus* distributed at shallowest depths of the three species peaking at 250 m year round. The most significant seasonal difference was the presence of higher densities at shallower depths, 200-350 m, during Jun-Nov for *A. denticulatus* and particularly for *A. minor* (Fig. 7). A similar seasonal shift with depth was not noted for *A. lupus*.

In addition to seasonal shifts, the distribution of *A. denticulatus* and *A. minor* varied with depth during the four periods of differing abundance. The differences were greatest during Jun-Nov (Fig. 7). During, the period of highest abundance, *A. denticulatus* and *A. minor* were more shallowly distributed than during the Decline or Low periods. The distribution during Current period more closely resembles the High period. A similar shift was not observed for *A. lupus*.

The manner in which average bottom temperature varied over time in relation to depth is illustrated in Fig. 8. During Dec-May, when bottom temperatures are expected to be coldest, values averaged 0.5-1.7° C at 0-50 m and -0.5-1.8° C between 101-150 m. Most of the coldest temperatures were observed on the Grand Bank and close to the coast northeast of Newfoundland. Temperature increased with depth, leveling off at ~3-4° C beyond 400 m (regardless of season). However, during Jun-Nov, shallow (0-50 m) bottom temperatures were considerably higher than during Dec-May, varying between 2 and 5°C depending on period observed (similar during this time at 101-150 m). One pattern of note is the significantly higher temperature observed from 150-450 m for the Pre period. However, not all areas were surveyed during that time which may have contributed to the higher values observed.

Figure 9 describes the spatial extent in km^2 of area covered by different bottom temperatures. About 35% of the shelf area was covered by bottom temperatures < 0°C and most of the remainder was in the range of 0.0°C to 5.0°C. The spatial extent of temperature ranges was similar between seasons with the greatest differences occurring near shore away from the centre of distribution of the wolffish species.

All three species are associated with a relatively narrow range of bottom temperatures and unlike depth, this association changed little over the period of the surveys, or seasonally (Fig. 10). One exception is the slightly higher densities observed in lower temperatures during Jun-Nov. *A. denticulatus* and *A. minor* reached their maximum density (kg per tow) at 2-5°C while *A. lupus* peaked in abundance at slightly lower temperatures (1-4°C).

An examination of fish density (average kg per tow) in regard to trawl fishing activity indicates that the rate of decline of fish density between fished vs. unfished locations was similar (Fig. 11). Density of each of the three wolffish species was observed to decrease at a greater extent during the period of greatest decline, from the mid-1980's to the early 1990's. *A. lupus* actually increased its density in the most intensely fished areas during the mid to late-1980s.

Wolffish distributions were modeled using a full GAM's with terms for temperature, depth, latitude and longitude and partial GAM model which excluded latitude and longitude. Lack of significant differences between the respective models for all three species indicated the lack of importance of spatial location relative to depth and temperature alone. Pseudo-R squared values for all three species ranged from 35% to 70%. Modeled distributions are presented in Figures 12 and 13 for *A. denticulatus* and *A. minor* respectively for select years. In both cases, the distributions show, similar to the analyses elaborated above, a restriction of wolffish distribution in periods of low abundance to deeper, warmer waters along the edge of the Grand Banks to the Labrador Shelf. During periods of high abundance, the distribution of both species is more widespread along shallower areas of the shelf.

During periods of high abundance, *A. denticulatus* and *A. minor* were distributed throughout the available temperature and depth regimes (Fig. 14-17). During periods of lower abundance, wolffish were distributed in warmer and deeper waters relative to the available environment.

Also, during periods of high abundance, wolffish are captured on all sediment types. However, during periods of low abundance, *A. denticulatus* appear to occur less frequently on mud or muddy substrates relative to the occurrence of sediments in the environment (Fig. 18-19). Overall, survey catch rates of *A. denticulatus* appear to be greater in areas defined as sand/shell/pebbles. Unlike *A. denticulatus*, *A. minor* and *A. lupus* appear to show little preference for any specific sediment type (Table 4).

Dive site descriptions and related descriptions of *A. lupus* abundance are summarized in Table 5. *A. lupus* were only observed in habitats with temperatures below 10° C, and temperatures below 0° C were tolerated. *A. lupus* was not observed in reduced salinity, at estuarine locations: they are always deeper than major haloclines. As well, they were never observed on soft bottoms composed of either mud or soft clay that can be easily stirred up. *A. lupus* reproduction appears, at least in inshore areas, to be dependent on the availability of boulders or caves for spawning. There is little wild larval and juvenile habitat information. Small fish were observed in the vicinity of dens during the winter, however paucity of information on timing of hatching limits information on residency in the vicinity.

Discussion

The three wolffish species are at the center of their distribution, reaching highest density and covering the largest area on the northeast Newfoundland and Labrador Shelf. There they distribute over a wide range of depths, from about 25 m to > 1 400 m. *A. denticulatus* occupying the widest range, *A. lupus* the narrowest. The area centered at Lat. 48° 30', Lon. 51° just north of the Grand Banks constitutes the most persistent location of high concentrations of all three species in the northwest Atlantic. The exception is a concentration of *A. lupus* on the southern Grand Bank with similar densities observed to the north but over a smaller area.

Although not directly comparable (independent, uncalibrated surveys), densities of the three species in the Bay of Fundy, on the Scotian Shelf and in the Gulf of St Lawrence are likely lower than in our study area. Densities in those areas would likely be similar or lower than what is found in the adjacent Laurentian Channel (area Laur, our study which separates the Grand Banks from the Scotian Shelf and is the outer extent of the Gulf of St. Lawrence) where densities are

several times to a magnitude lower than the rest of our study area. Wolffish are also taken in a lower proportion of survey sets compared to our study area (McRuer et al. 2001).

Wolffish have undergone significant changes in their distribution. Both potential map and GAM distributions illustrated the range reduction in the distribution of wolffish during the periods of lowering abundance. It is a combination of change in area occupied and degree of concentration of biomass that has resulted in the changes in abundance reported by Simpson and Kulka (2002). The observed changes were greatest at the center of distribution of the three species, on the northeast Newfoundland and Labrador Shelves. There, this study has identified both a reduced area occupied and a reduction in density within the remaining areas during the 1990's compared to the late 1970's to early 1980's. In contrast, there was no significant reduction observed for *A. lupus* in terms of area occupied or abundance on the southern Grand Bank (Simpson and Kulka 2002) or other fringe locations. McRuer et al. (2001) noted an increase in abundance after the late 1980's in the Gulf of St. Lawrence and on the Scotian Shelf.

Our study has shown that temperature is an important feature of wolffish habitat. Changes in temperature have affected distribution if not abundance. All three species are associated with a narrow thermal range of above average bottom temperatures, mainly 1.5-4.5^{0}C, absent where temperatures are < 0^{0}C. This explains why they do not occur on the northern Grand Bank or the banks northeast of the island of Newfoundland where sub-zero temperatures occur year round. More specifically in terms of location, the inner portion of the shelf, where all three species underwent their greatest reduction, corresponded to the coldest areas of the range of each of the three species. At their lowest abundance (1990-1995), each of the species was restricted mainly to the warmest locations available along the outer shelf and it was during this period that some of the lowest bottom temperatures were recorded (Colbourne et al 2004). It is notable that *A. minor* and particularly *A. denticulatus* which underwent the greatest declines in abundance (Simpson and Kulka 2004) were more narrowly distributed at the center of their temperature range during the period of lowest abundance. One could speculate that unfavourable temperatures over a part of the range could restrict the population size of wolffish.

Based on the results of this study, wolffish may be classified as "temperature keepers" (sensu Perry and Smith 1994) – they maintain a similar temperature range by changing their depth distribution, as opposed to a depth-keeper such as yellowtail flounder (Perry and Smith 1994) who tolerate a wide range of temperature variation while maintaining their depth distribution. As well, based on focal animal observations of *A. lupus* near shore, it has been observed that they always occur deeper than major haloclines in estuarine locations and thus may not be tolerant of low salinity.

Range contraction during periods of declines in abundance have been observed in a number of other species in the northwest Atlantic including yellowtail flounder (Simpson and Walsh 2004) and Atlantic cod (Swain and Wade 1993, Atkinson et al 1997). Simpson and Walsh (2004) suggested that for yellowtail flounder, the observed patterns of range contraction and expansion were consistent with MacCall's basin hypothesis (MacCall 1990), where during periods of low abundance, fish concentrated in "preferred" habitats as density-dependent effects declined. For wolffish, future analysis of any range expansion in relation to abundance and bottom temperature will assist in elucidating this relationship. A slight increase in range, concurrent with small increases in abundance has already been observed for *A. lupus* and *A. minor*.

In addition to associations with temperature, depth and salinity, the distribution of wolffish is also related to sediment type. Based on direct observations of *A. lupus* in near-shore areas, they avoid areas where sediments can be stirred up such as on muddy substrates. As well, boulder areas where eggs can be deposited are also required during a part of the life cycle, at least in inshore locations (Keats et al 1985 and this study). In contrast, analysis of bottom type data using

ROXANN data indicated that *A. minor* and *A. lupus* were widely distributed on various sediment types. *A. denticulatus*, however, did occupy sand/shell hash, gravely sand and rock sediments more frequently than the occurrence of those sediment types in the environment would suggest. Conflicting results from individual and large scale methods emphasizes the difficulty in resolving critical habitat features in oceanic areas outside the shallow inshore zone. In addition, observed associations of wolffish with particular sediments, temperatures or depths may be related to additional factors with which these habitat variables are associated such as prey distribution or other environmental factors. Untangling these associations to determine habitat elements that are critical to wolffish may require experimentation.

Unlike the other two species, there is a concentration of *A. lupus* on the south central part of the Grand Bank at shallow depths (< 150 m). Bottom temperatures there are relatively warm, within the preferred range of all three species so temperature does not explain the absence of *A. denticulatus* and *A. minor* from this area. Bottom type at that location comprises gravel fining to sand which based on our analyses appears suitable to be habitat for all three species. However, Kulka (1991), based on observations by Gordon Fader noted that this is an area where large boulders occur. Ours and other near shore observations indicate that *A. lupus* are dependent on the availability of boulders or caves for spawning and perhaps during other times. This association has not been observed for the other two species.

The area where wolffish were concentrated corresponds to the most heavily fished grounds along the outer shelf (Kulka and Pitcher 2001). The rate of decline at the unfished locations was observed to be similar or higher than in the most intensely fished areas. Thus, there is no evidence of cropping down by the fisheries. However, it appears that changes in ambient temperature, resulted in a greater proportion of the wolffish being concentrated on the outer shelf where fishing intensity was greatest, thus making the remaining fish more vulnerable to exploitation.

Conclusions

The Species at Risk Act (SARA) recognizes that habitat is an important component for survival and recovery of species designated as at risk. However, direct observations of physical habitat associations for widely distributed, oceanic species, such as wolffish, is problematic. Determining what is critical to survival of a species in an enclosed and directly observable environment such as a marsh or pond is far less complicated than for species that inhabit vast expanses of the unobservable ocean habitat. Three factors impede the definition of critical habitat in the open ocean in general and for wolffish in particular. First, deficient knowledge of wolffish life history, second, limited information on the influence of multi-scale processes upon wolffish population dynamics, and finally the lack of information on acceptable targets for wolffish population abundance and range. Consequently it is difficult to define critical habitats for wolffish, particularly since each developmental stage may have different requirements that are at present unknown.

This study has however determined that wolffish are temperature keepers undergoing substantial distributional changes, at least in part in response to changes in bottom temperature. For wolffish, habitat preference is perhaps best conceptualized as a range of ambient temperatures rather than as a particular physical location. Translation of appropriate thermal conditions to a physical location as a preferred habitat could be viewed as the (reduced) area occupied by the species when abundance was lowest. It is this area that maintained thermal conditions most appropriate for survival of the species, not the case over the entire distribution of the species.

Just as the clear cutting of old growth forest is linked to the survival of the burrowing owl, the absence of a suitable range of temperatures over the shelf could result in the disappearance of wolffish from those areas. A key difference between these two scenarios is that the disappearance

of old growth forest habitat is human induced while changes in bottom temperatures would largely be a natural phenomenon. This study has not established a clear link to survival or the proximal causes of change in habitat but it has demonstrated that thermal conditions appear to affect population abundance.

The following can be concluded about wolffish species at the centre of their concentration in Canadian waters in relation to the TOR for this workshop series:

- Distributions and abundance indices of wolffish can be derived from survey data. Variation in the annual spatial coverage of the surveys (i.e. Northern area not sampled in many years) places some limits on the information – particularly for *A. denticulatus* and *A. minor* which have a more northerly and deeper distribution than *A. lupus*.
- Change in survey gear in 1995/1996 from the Engel's to Campelen trawls, and lack of comparative surveys and size based conversion factors between the gear types, has resulted in a truncated abundance index. Consequently, even simple PVA models cannot be employed due to the lack of an adequate time series (< 9 years). Demographic data are presently lacking for these species (research in progress).
- While individual scale observations of *A. lupus* in inshore areas indicate a preference for boulder/rocky areas for spawning and avoidance of muddy substrates – comparable data are not available for the analysis for the other two species or for *A. lupus* over much of its area of distribution. Consequently, HSP models, based on suitability functions are problematic since inadequate individual scale habitat information exists for the majority of the species range. In addition, there is a dynamic aspect to temperature regimes at multiple spatial/temporal scales which at present have not been modelled.
- While wolffish can be associated with various depth and temperature profiles, in particular temperature – the multi-scale spatial and temporal variations in these variables are problematic in utility for defining critical habitat.

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Table 1. Accounting of survey sets used in the study. Refer to Simpson and Kulka 2002 for an accounting of trends in abundance upon which the population status year groupings were based. Upper table: by month and period. Lower table: by area (refer to Fig. 1) and period. Areas: Norlab – Labrador Shelf, the area north of Lat. 55° 30'; Lab – Labrador Shelf north of Lat. 55° 30' and south of Lat. 55° 30'; GB – Grand Banks; Laur – Laurentian Channel, west of Lon. 56°

	1971-1977 Pre	1978-1984 High	1985-1989 Decline	1990-1995 Low	1995-2003 Recover	Total
Jan	20	49	63	157	396	685
Feb	4	218	473	947	260	1,902
Mar	108	838	495	197	88	1,726
Apr	439	816	818	1,072	1,672	4,817
May	589	1,001	1,524	1,579	1,442	6,135
Jun	267	709	357	766	1,689	3,788
Jul	9	899	205	346	84	1,543
Aug	26	594	417	115	301	1,453
Sep	5	327	103	141	400	976
Oct	17	878	882	574	2,336	4,687
Nov	138	1,363	1,314	2,219	2,851	7,885
Dec	6	395	375	761	1,502	3,039
	1,628	8,087	7,026	8,874	13,021	38,636
Jan	1.2%	0.6%	0.9%	1.8%	3.0%	1.8%
Feb	0.2%	2.7%	6.7%	10.7%	2.0%	4.9%
Mar	6.6%	10.4%	7.0%	2.2%	0.7%	4.5%
Apr	27.0%	10.1%	11.6%	12.1%	12.8%	12.5%
May	36.2%	12.4%	21.7%	17.8%	11.1%	15.9%
Jun	16.4%	8.8%	5.1%	8.6%	13.0%	9.8%
Jul	0.6%	11.1%	2.9%	3.9%	0.6%	4.0%
Aug	1.6%	7.3%	5.9%	1.3%	2.3%	3.8%
Sep	0.3%	4.0%	1.5%	1.6%	3.1%	2.5%
Oct	1.0%	10.9%	12.6%	6.5%	17.9%	12.1%
Nov	8.5%	16.9%	18.7%	25.0%	21.9%	20.4%
Dec	0.4%	4.9%	5.3%	8.6%	11.5%	7.9%

	1971-1977 Pre	1978-1984 High	1985-1989 Decline	1990-1995 Low	1995-2003 Recover	Total
Norlab		531	385	80	589	1,585
Lab	358	3,631	2,464	3,291	4,094	13,838
GB	900	3,329	3,499	4,537	7,196	19,461
Laur	370	595	678	969	1,137	3,749
Total	1,628	8,086	7,026	8,877	13,016	38,636
Norlab	0.0%	6.6%	5.5%	0.9%	4.5%	4.1%
Lab	22.0%	44.9%	35.1%	37.1%	31.5%	35.8%
GB	55.3%	41.2%	49.8%	51.1%	55.3%	50.4%
Laur	22.7%	7.4%	9.6%	10.9%	8.7%	9.7%

Table 2. Area occupied statistics for the three species of wolffish. Upper panel of the table shows area in km^2. Lower panel shows percent of total area (see fig. 2a). Lower table shows two areas for *A. lupus*.

	A. denticulatus					*A. minor*					*A. lupus*				
						Area (km^2)									
Density	**Pre**	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**
0	268,700	265,242	373,708	481,582	516,230	266,942	320,438	385,866	463,331	463,961	203,110	279,203	323,062	371,308	293,577
Low	12,768	50,694	57,696	58,140	142,636	8,810	46,092	53,155	52,980	150,059	13,150	49,841	51,429	67,313	240,216
Medium	23,862	93,561	96,752	52,146	14,671	20,536	77,886	87,597	57,525	50,421	61,571	125,079	133,345	120,913	125,468
High	68,622	210,417	85,422	5,963	0	77,599	175,510	86,996	23,952	9,077	95,913	165,853	105,730	38,274	14,250
Area Occupied	105,252	354,672	239,870	116,249	157,307	106,945	299,488	227,748	134,457	209,557	170,634	340,773	290,504	226,500	379,934
	Pecent of Total Area Surveyed														
	Pre	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**
0	71.9%	42.8%	60.9%	80.6%	76.6%	71.4%	51.7%	62.9%	77.5%	68.9%	54.3%	45.0%	52.7%	62.1%	43.6%
Low	3.4%	8.2%	9.4%	9.7%	21.2%	2.4%	7.4%	8.7%	8.9%	22.3%	3.5%	8.0%	8.4%	11.3%	35.7%
Medium	6.4%	15.1%	15.8%	8.7%	2.2%	5.5%	12.6%	14.3%	9.6%	7.5%	16.5%	20.2%	21.7%	20.2%	18.6%
High	18.4%	33.9%	13.9%	1.0%	0.0%	20.8%	28.3%	14.2%	4.0%	1.3%	25.6%	26.8%	17.2%	6.4%	2.1%
Area Occupied	28.1%	57.2%	39.1%	19.4%	23.4%	28.6%	48.3%	37.1%	22.5%	31.1%	45.6%	55.0%	47.3%	37.9%	56.4%
	Percent of Area Occupied														
	Pre	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**
Low	12.13%	14.29%	24.05%	50.01%	90.67%	8.24%	15.39%	23.34%	39.40%	71.61%	7.71%	14.63%	17.70%	29.72%	63.23%
Medium	22.67%	26.38%	40.34%	44.86%	9.33%	19.20%	26.01%	38.46%	42.78%	24.06%	36.08%	36.70%	45.90%	53.38%	33.02%
High	65.20%	59.33%	35.61%	5.13%	0.00%	72.56%	58.60%	38.20%	17.81%	4.33%	56.21%	48.67%	36.40%	16.90%	3.75%

	A. lupus North of Lat 48					*A. lupus* Grand Banks				
					Area (km^2)					
Density	**Pre**	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**
0	39,306	98,038	130,987	170,381	165,264	53,380	44,324	39,688	43,806	19,655
Low	2,592	24,461	26,258	28,143	107,768	2,591	6,349	8,331	12,857	49,521
Medium	19,007	62,748	83,022	77,058	79,138	15,144	25,984	21,111	18,847	16,367
High	66,172	139,355	77,045	22,777	11,357	6,754	8,318	16,213	10,007	6
Area Occupied	87,771	226,564	186,325	127,978	198,263	24,489	40,651	45,655	41,711	65,893
	Percent of Total Area Surveyed									
	Pre	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**
0	30.9%	30.2%	41.3%	57.1%	45.5%	68.6%	52.2%	46.5%	51.2%	23.0%
Low	2.0%	7.5%	8.3%	9.4%	29.6%	3.3%	7.5%	9.8%	15.0%	57.9%
Medium	15.0%	19.3%	26.2%	25.8%	21.8%	19.4%	30.6%	24.7%	22.0%	19.1%
High	52.1%	42.9%	24.3%	7.6%	3.1%	8.7%	9.8%	19.0%	11.7%	0.0%
Area Occupied	69.1%	69.8%	58.7%	42.9%	54.5%	31.4%	47.8%	53.5%	48.8%	77.0%
	Percent of Area Occupied									
	Pre	**High**	**Decline**	**Low**	**Current**	**Pre**	**High**	**Decline**	**Low**	**Current**
Low	2.95%	10.80%	14.09%	21.99%	54.36%	10.58%	15.62%	18.25%	30.82%	75.15%
Medium	21.66%	27.70%	44.56%	60.21%	39.92%	61.84%	63.92%	46.24%	45.18%	24.84%
High	75.39%	61.51%	41.35%	17.80%	5.73%	27.58%	20.46%	35.51%	23.99%	0.01%

Table 3. Area occupied statistics for three species of wolffish comparing potential area, which is currently not occupied but was previously occupied, and the current area occupied. (values in km^2).

	A. denticulatus	A. minor	A. lupus
Potential	230,399	136,627	58,565
Current	154,941	209,556	379,934
Total	385,340	346,183	438,499
	A. denticulatus	**A. minor**	**A. lupus**
Potential	60%	40%	13%
Current	40%	61%	87%
Total	100%	100%	100%

Table 4. Summary of the average number of wolffish captured per tow in relation to sediment type.

Average number of Northern wolffish per tow in relation to sediment type in select years

1978	1982	1987	1992	1997	2002	
3.00	1.50	0.33	0.00	0.00	0.00	**1 - mud**
2.20	0.86	0.42	0.24	0.06	0.14	**2 - sand**
3.08	1.33	0.36	0.19	0.12	0.17	**3 - sand & shell**
1.20	0.78	0.06	0.09	0.22	0.20	**4 - shell & pebbles**
3.38	0.36	0.11	0.04	0.08	0.07	**5 - small rock**
1.15	0.50	0.10	0.04	0.04	0.05	**6 - hard bottom**

Average number of Atlantic wolffish per tow in relation to sediment type in select years

1978	1982	1987	1992	1997	2002	
8.00	2.33	0.67	0.17	0.09	0.11	**1 - mud**
8.83	2.17	2.23	0.47	0.87	0.46	**2 - sand**
9.65	2.42	1.45	1.01	0.44	1.18	**3 - sand & shell**
6.22	0.61	0.19	0.91	0.77	1.28	**4 - shell & pebbles**
14.75	1.29	1.50	0.81	1.55	1.58	**5 - small rock**
2.85	1.11	1.33	0.36	0.47	2.09	**6 - hard bottom**

Average number of Spotted wolffish per tow in relation to sediment type in select years

1978	1982	1987	1992	1997	2002	
0.43	0.17	0.33	0.00	0.18	0.38	**1 - mud**
0.90	2.03	0.42	0.34	0.24	0.26	**2 - sand**
1.07	0.92	0.41	0.17	0.12	0.35	**3 - sand & shell**
1.56	1.35	0.16	0.25	0.18	0.37	**4 - shell & pebbles**
2.00	0.56	0.42	0.09	0.12	0.11	**5 - small rock**
1.54	0.74	0.50	0.05	0.04	0.32	**6 - hard bottom**

Table 5. Summary of *A. lupus* abundance and dive site characteristics as derived from SCUBA surveys undertaken on the coast of western Newfoundland.

Location	Substrate	Oceanography	Biology	Wolffish
Bonne Bay				
Man of War Cove	Bedrock limestone outcrops from the surface to c 6m depth, boulders and gravel to 10m, fine silt, clay below 10m becoming muddier (finer) with depth. Sediments easily stirred up	Surface estuarine, temperature and salinity highly stratified, permanently cold (near 0 below estuarine zone), highly sheltered from wave energy	Biology. Attached seaweeds, mussels, hydrozoans on rocks. Biota below 10m dominated by *Arctica*, polychaetes worms and other infauna	None
Gull Rock	Shale outcrops with gullies and cliffs to 25m, boulders from 20 to 27m, shell hash and highly biogenous course to fine sands below 27m. Sediments quite clean	Surface estuarine, temperature and salinity highly stratified, moderate seiche currents < 25 $cmsec^{-1}$, wave effects limited to shallow water above 5m depth	Shallow, <5m depth zone rich estuarine communities of seaweeds, blue mussels, cunners, etc. Kelp beds start at 5m, below influence of reduced salinity, horse mussels, coralline algae, sponges, chitons abundant. Below 15m coldwater loving arctic species of seaweeds and animals become abundant	Usually 1 or 2 observed per dive sitting alone on the bottom among the boulders and shell hash. Two pairs observed in September and October in dens excavated under large boulders
Norris Cove	seabed is a steep bed of course sand, fine gravel and anthropogenic debris	subject to strong (up to 50 $cmsec^{-1}$) tidal currents and internal waves. The surface waters are subject to relatively reduced salinity on the ebb tides and notably higher salinity on flood tides. Water mass stratification by temperature and salinity is pronounced with pycnoclines near the surface, at about 15m and about 25m depth	Winter flounders, *Pleuronectes*, *Myoxocephalus* spp., sculpins, skates, *Raja* spp. and cunners, *Tautogolabrus* are most common. In depths below 20m American plaice were abundant. The most common invertebrates were green sea urchins, brittle stars, crabs *Cancer* and *Hyas*, the hermit crabs, *Pagurus* spp., sand dollars, *Echinarachnius*, bivalve molluses *Astarte*, *Placopecten* and *Modiolus* and several infaunal polychaetes	Wolffish observed on virtually every dive between May and November. Wolffish usually resting on the sandy substratum and were either feeding or had relatively distended abdomens indicating recent feeding. The same wolffish was observed for several consecutive dives resting in the same location. Fresh piles of crushed shells near this fish were considered to be fecal material
Gadds Point	The seabed is a very steep slope composed of shale cliffs, outcrops and large shale boulders. Below about 15m there are large amounts of shell gravel and biogenous sand between and below the rocks	Strong tidal currents, sometimes over 80 $cmsec^{-1}$ sweep over these rocks, especially during spring flood tides. Fluctuations in salinity and water column stratification are similar to those at Norris Cove	Rock surfaces are totally covered by seaweeds and sessile animals such as mussels, anemones, hydrozoans and sponges. Highest biodiversity of any site in Newfoundland incl. migratory pelagic fish here including pollack, haddock, dogfish, hake, herring, cod, herring, and mackerel	Wolffish were abundant here in the late 1970's
Bonne Bay sill	Subtrate is variable. Some shallow portions are covered by rippled fine to coarse sand. Outer and inner slopes have	Water flows governed by tidal forces which carry large amounts of estuarine surface water	Associated fish include Eel pouts, winter flounder, cunners,	Large numbers of individual wolffish were observed here, especially on the coarse sand and

	areas of ice dropped boulders. Eroding portions of the sill are largely gravel where strong currents have winnowed away the finer sediments. The central channel of the sill is occupied by extensive areas of rhodoliths of the coralline algae, *Lithothamnion glaciale* and *Lithothamnion tophiforme*.	offshore during ebb tides and carry more oceanic waters in during flood tides. The surface and seabed currents are out of phase so that surface seaward flow becomes quite strong while deepwater currents are still flowing into the bay. These high energy processes lead to a great deal of seawater mixing and the estuarine stratification characteristic of the inner fjord ceases at the sill.	shannies, and skate. Rocks are all covered with coralline algae and frequently by kelps. Sandy areas support large numbers of sand dollars and *Arctica* clams. Rhodolith areas include large numbers of brittle stars, polychaetes and crabs.	gravel areas including the rhodoliths beds. A few breeding dens were observed under boulders but this areas is hard to census because of the strong currents.
Pinnacle Point	The shallow seabed is covered by large boulders down a steep slope to about 15m depth. There is a sharp boundary between the lower margin of the boulders and the start of a sand slope that continues down to over 100 m depth.	Stratification is less extreme than within the inner fjord but there is still a considerable temperature decline with depth at this site. Salinity is usually quite oceanic at all depths. Currents are moderate and usually flow from the Gulf into the bay and are strongest on the flood tides. These currents are frequently nutrient rich and productive. Wave energy is considerably higher here than in the previously described sites.	Productive giant kelp beds and high diversity of plants and animals associated with this habitat. The area is heavily exploited by fishermen harvesting lobsters, snow crab, mackerel and other species.	Wolffish are especially abundant here in the spring when snow crab migrate into shallow water.
Salmon Point	Exposed to the open Gulf of St Lawrence west of Rocky Harbour. The seabed is composed of limestone and shale outcrops with patches of boulders and mobile patches of coarse sand.	Although surface salinity may be slightly reduced, this area is usually fully saline. Wave energy is extreme, as the site is totally exposed to the prevailing westerly winds. Strong ebb currents flow out of Bonne Bay past this point. Pack ice grounds here during severe winters and heavily scours the substratum and relocates large boulders.	Biodiversity and productivity are reduced at this site because of the ice and storm mortality. Much of the substratum is denuded and becomes occupied by early stage successional species. A few lobsters shelter under boulders. Cunners are much less abundant than at other sites. Kelp beds sometimes develop sparsely. Sea urchins are extremely abundant but are small because of the high mortality rates.	Single wolffish 10 dives.
Avalon Peninsula				
Bay Bulls	Shallow habitat to 6m depth is dominated by bedrock. Below this are large boulders, outcrops and patches of boulders, gravel and rhodoliths. Rhodoliths and mobile patches of shell hash coarse sand become abundant at depths below 20 m though boulders and outcrops are still abundant.	An upwelling shore during the prevailing southwesterly winds of summer. Conditions are frequently colder than normal for Newfoundland in the summer. Salinity is high. Coast subject to heavy groundswell waves that originate from distant weather systems. These long waves create strong	Kelp beds dominate the shallow surf zone but bushy seaweed cover is much reduced below 3m due to presence of sea urchins. Rocks covered heavily by coralline algae. Subtidal seaweed beds patchy, mainly in vicinity of large boulders. Abundant 'pops' of northern whelks.	Observed breeding wolffish in the early 1970's. Located 14 dens in a local area of less than 1 hectare in 1978.

		oscillating currents even at depths below 30m in contrast to the Gulf of St Lawrence waves that have only shallow effects	limpets, *Hyas* crabs, *Leptasterias* seastars and *Asterias*. In depths below 15m *Tealia* anemones are abundant and iceland scallops are present below 30m	
Portugal Cove	Bedrock outcrops dominate the first 3 or 4 meters off Portugal Cove. Patches of boulders occur at the base of the bedrock and are followed by sand and gravel patches that extend to about 12m where they are replaced predominantly by rhododoliths and scattered boulders and outcrops	Portugal Cove is subject to downwelling with warm water extending quite deeply during the summer. This site is usually more sheltered from offshore storm waves except for those that sometimes come from the north, especially in the fall. Salinity is usually over 30 salinity units	Shallow fringe of seaweeds occurs around the low tide level but this is frequently eradicated by sea urchins during the summer. Sea urchins, common periwinkles and acoel flatworms are the most prominent animals on rocks to about 10m depth. Coralline algae and *Asterias* become more abundant with depth. Rhodoliths of *Lithothamnion glaciate* grow up to 30cm in diameter and sheltered a highly diverse biota of invertebrates and algae. Sandy patches contain numerous sand dollars. Cunners, Atlantic eel pout, winter flounder and skates are the most common fish	Solitary wolffish rarely observed below the summer thermocline at this site in fully saline water below 10°C. No breeding dens have been observed here. Several breeding dens have been found north of here closer to Bauline

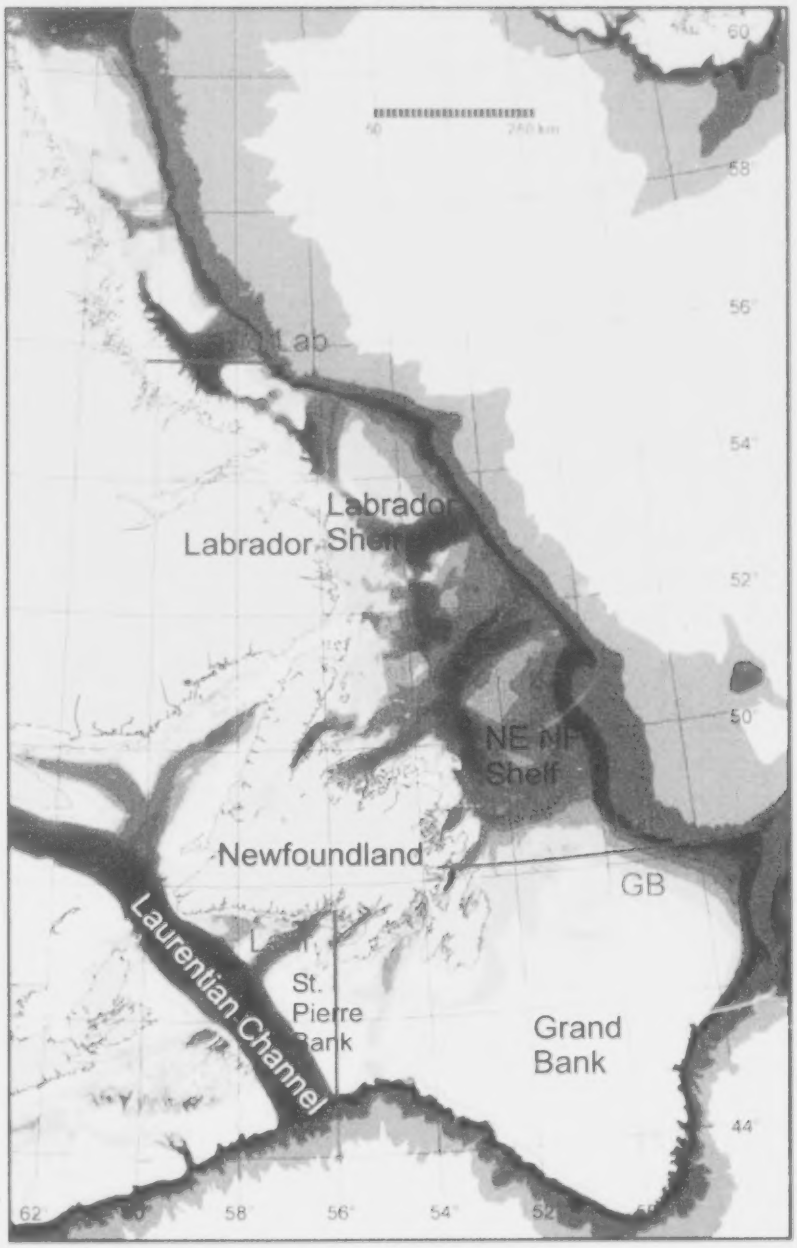

Figure 1. Study area. Blue shades represent bathymetry; white, 0-50 m grading to darkest blue, 901-1000 m. Dark grey is 1001-2000 m, lighter grey, 2001-3000 m, lightest grey, > 3000 m.

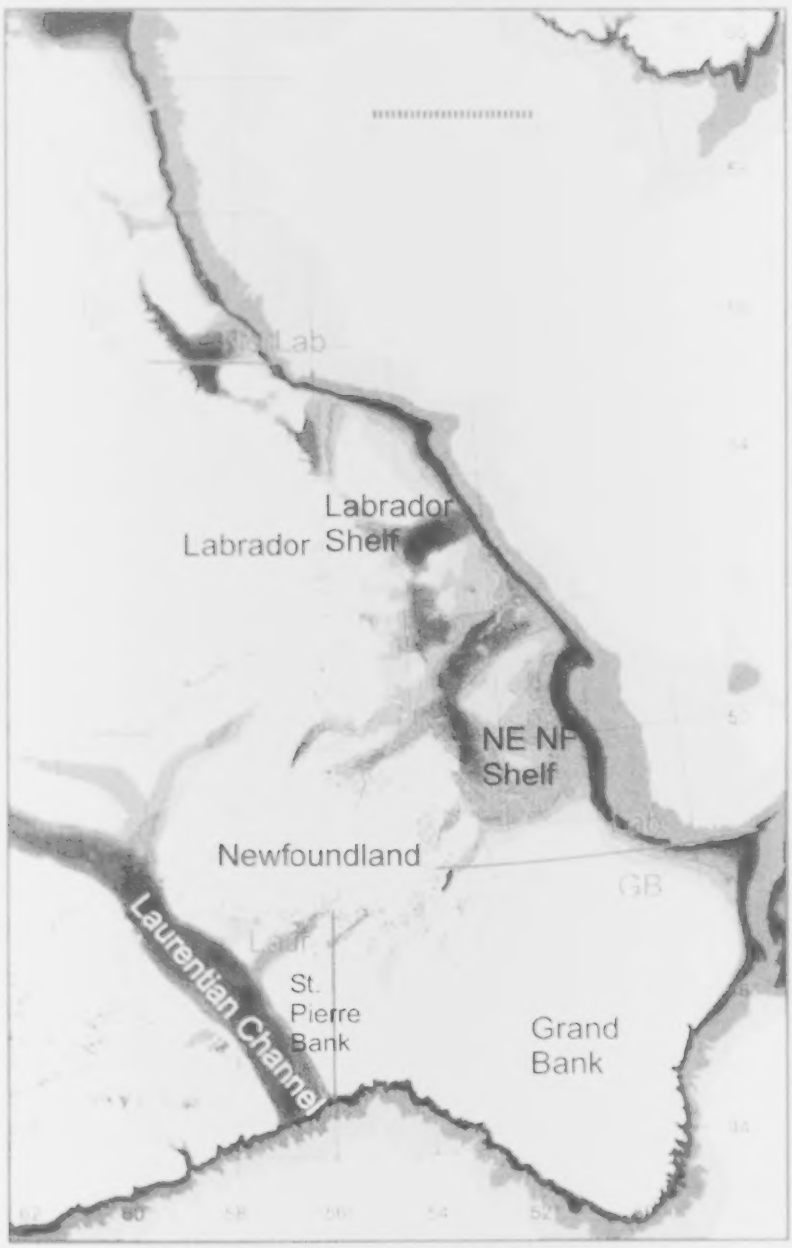

Figure 1. Study area. Blue shades represent bathymetry; white, 0-50 m grading to darkest blue, 901-1000 m. Dark grey is 1001-2000 m, lighter grey, 2001-3000 m, lightest grey, >3000 m.

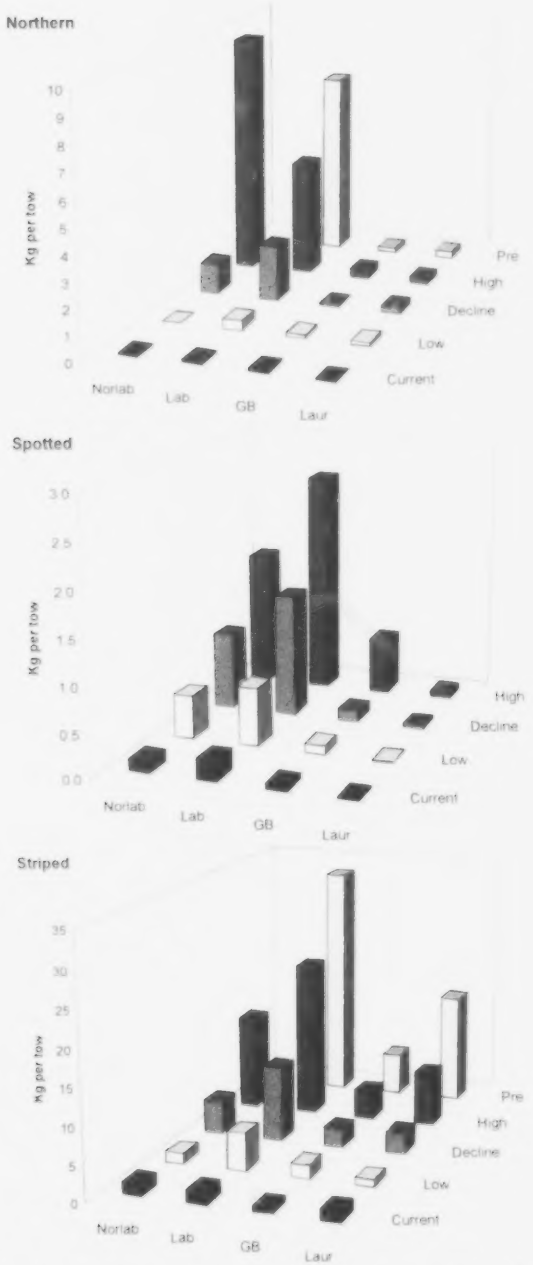

Figure 2. Average density (kg per tow) by area and time period. Refer to Fig. 1 for a definition of areas. Periods: Pre – 1971-1977, High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003. Norlab – Labrador Shelf, the area north of Lat. 55° 30'; Lab – Labrador Shelf north of Lat. 55° 30' and south of Lat. 55° 30'; GB – Grand Banks; Laur – Laurentian Channel, west of Lon. 56° (refer to Fig. 1).

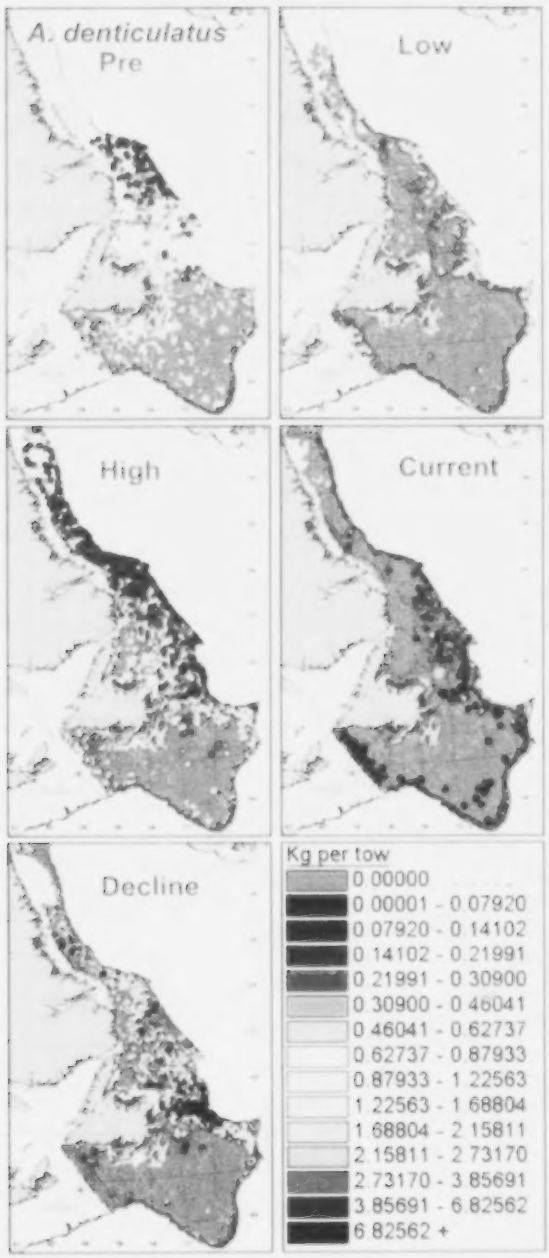

Figure 3a. Distribution of ***A. denticulatus*** on the Grand Banks, northeast Newfoundland and Labrador Shelves. Distributions are derived from DFO trawl surveys. Sets occurred during all 12 months but the majority were from the spring and fall. Five periods were delineated according to state of the population: Pre – 1971-1977, High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003.

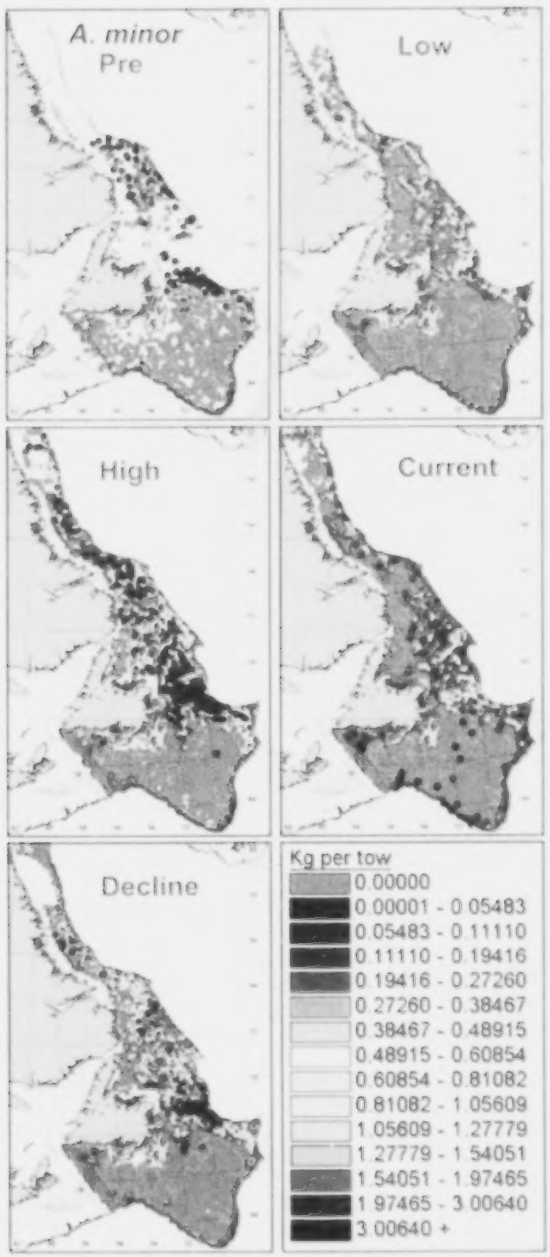

Figure 3b. Distribution of ***A. minor*** on the Grand Banks, northeast Newfoundland and Labrador Shelves. Distributions are derived from DFO trawl surveys. Sets occurred during all 12 months but the majority were from the spring and fall. Five periods were delineated according to state of the population: Pre – 1971-1977, High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003.

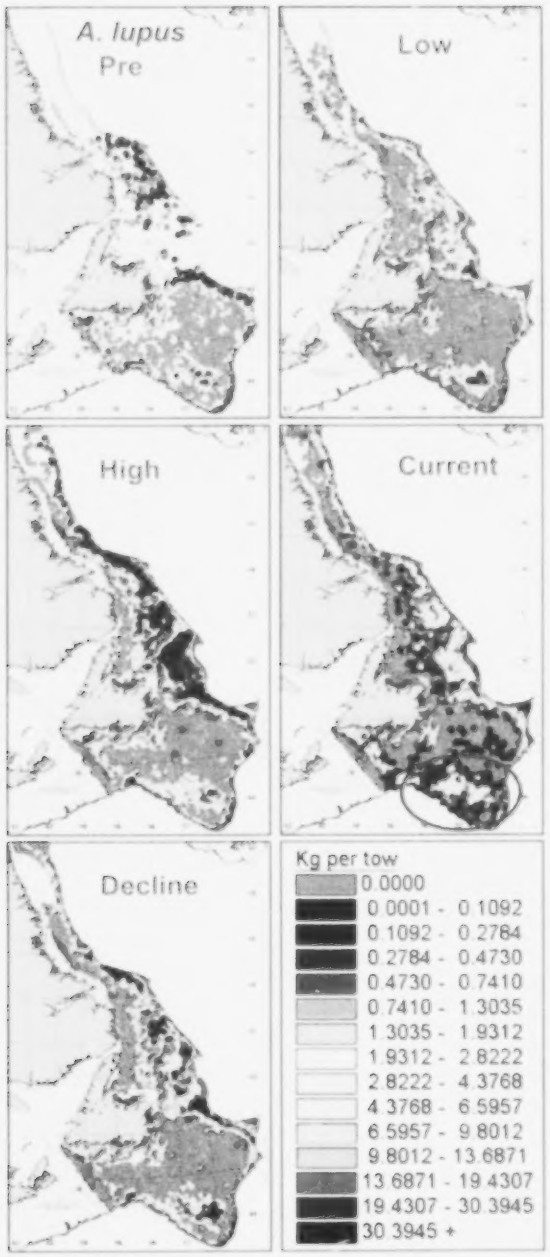

Figure 3c. Distribution of ***A. lupus*** on the Grand Banks, northeast Newfoundland and Labrador Shelves. Distributions are derived from DFO trawl surveys. Sets occurred during all 12 months but the majority were from the spring and fall. Five periods were delineated according to state of the population: Pre – 1971-1977, High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003. Orange circle on "Current" delineates the Grand Banks concentration (see Fig. 3b).

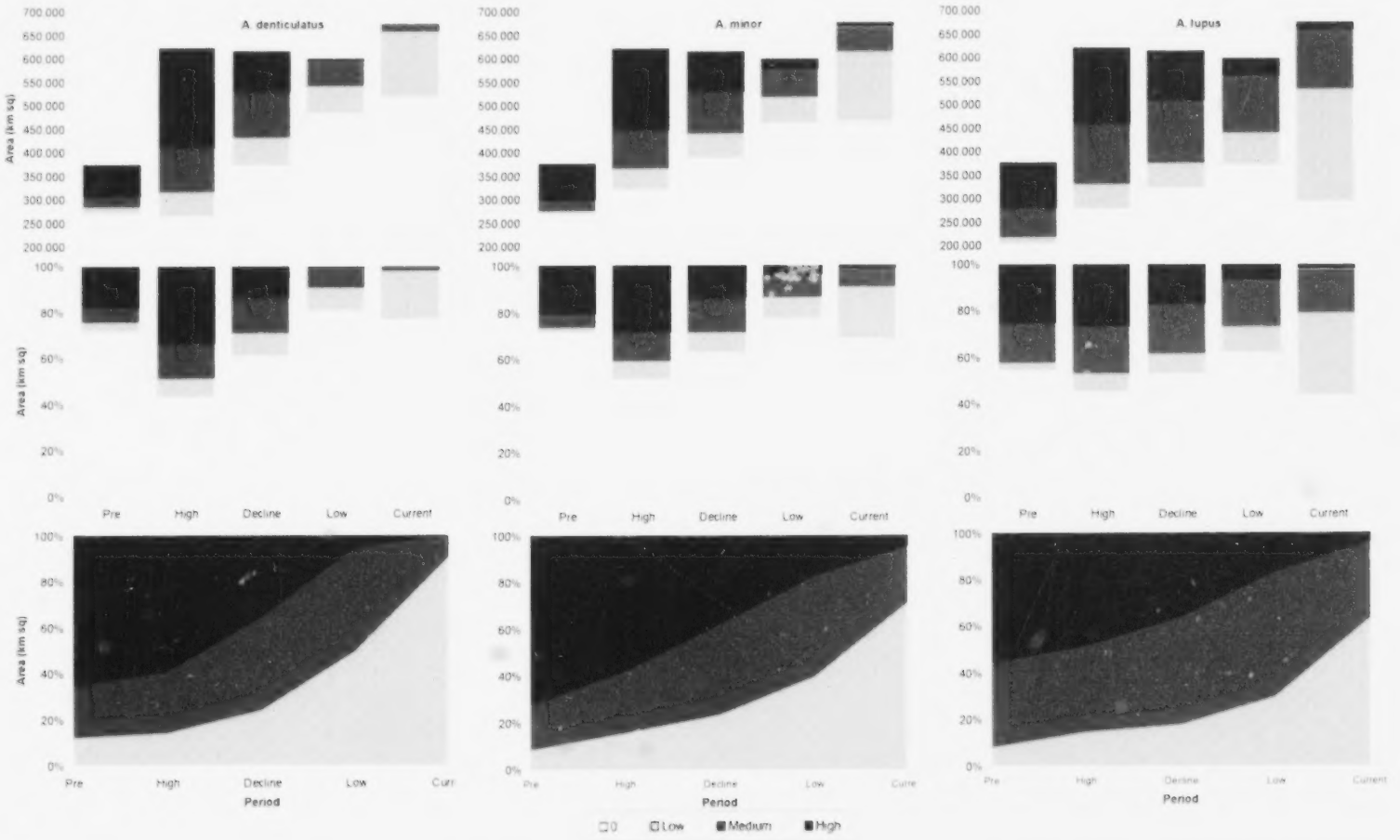

Figure 4a. Changes in **area occupied (upper panels)** and **degree of concentration** (lower panels): *A. denticulatus* – High >2.2 kg per tow; Med 1.5-2.2; Low 0.1-1.5. *A. minor* – High >1.3 kg per tow; Med 0.4-1.3; Low 0.1-1.3. *A. lupus* – High >9.8 kg per tow; Med 1.3-9.8; Low 0.1-1.3. White portions of the bars represent the are surveyed that contain no wolffish.

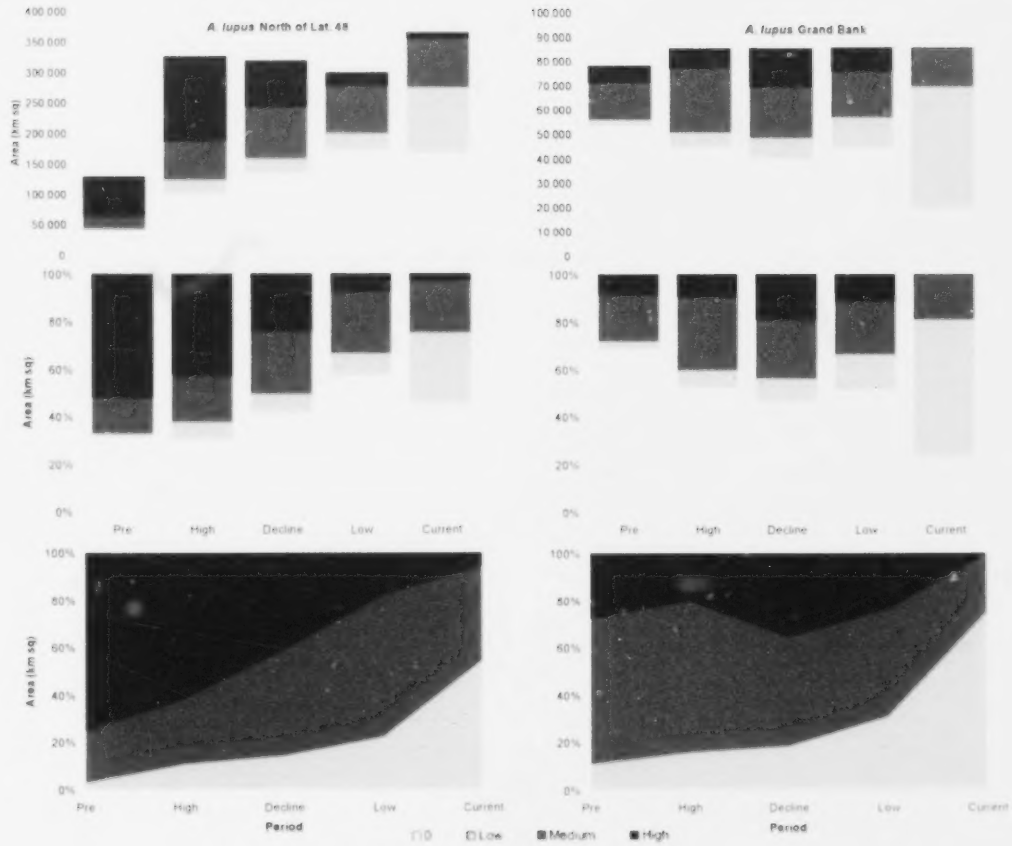

Figure 4b. Changes in **area occupied** (upper panels) and **degree of concentration** (lower panels): north of Lat. 48°:compared to the southern Grand Bank concentration (delineated in Fig. 2c): *A. lupus* – High >9.8 kg per tow; Med 1.3-9.8; Low 0.1-1.3.

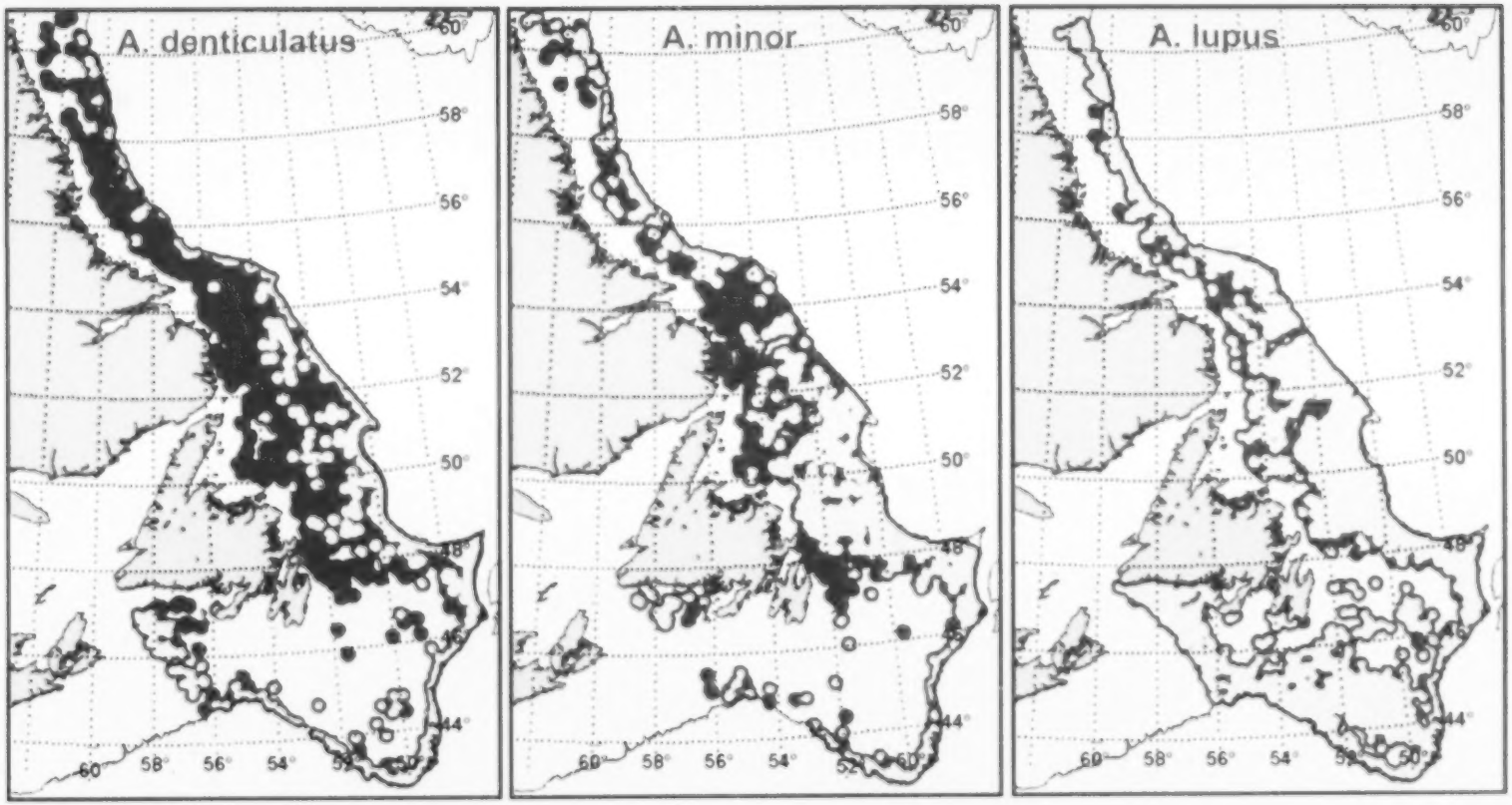

Figure 5. Potential habitat. Locations where wolffish occurred during the High period but are no longer present are represented in red. Yellow shows present area occupied.

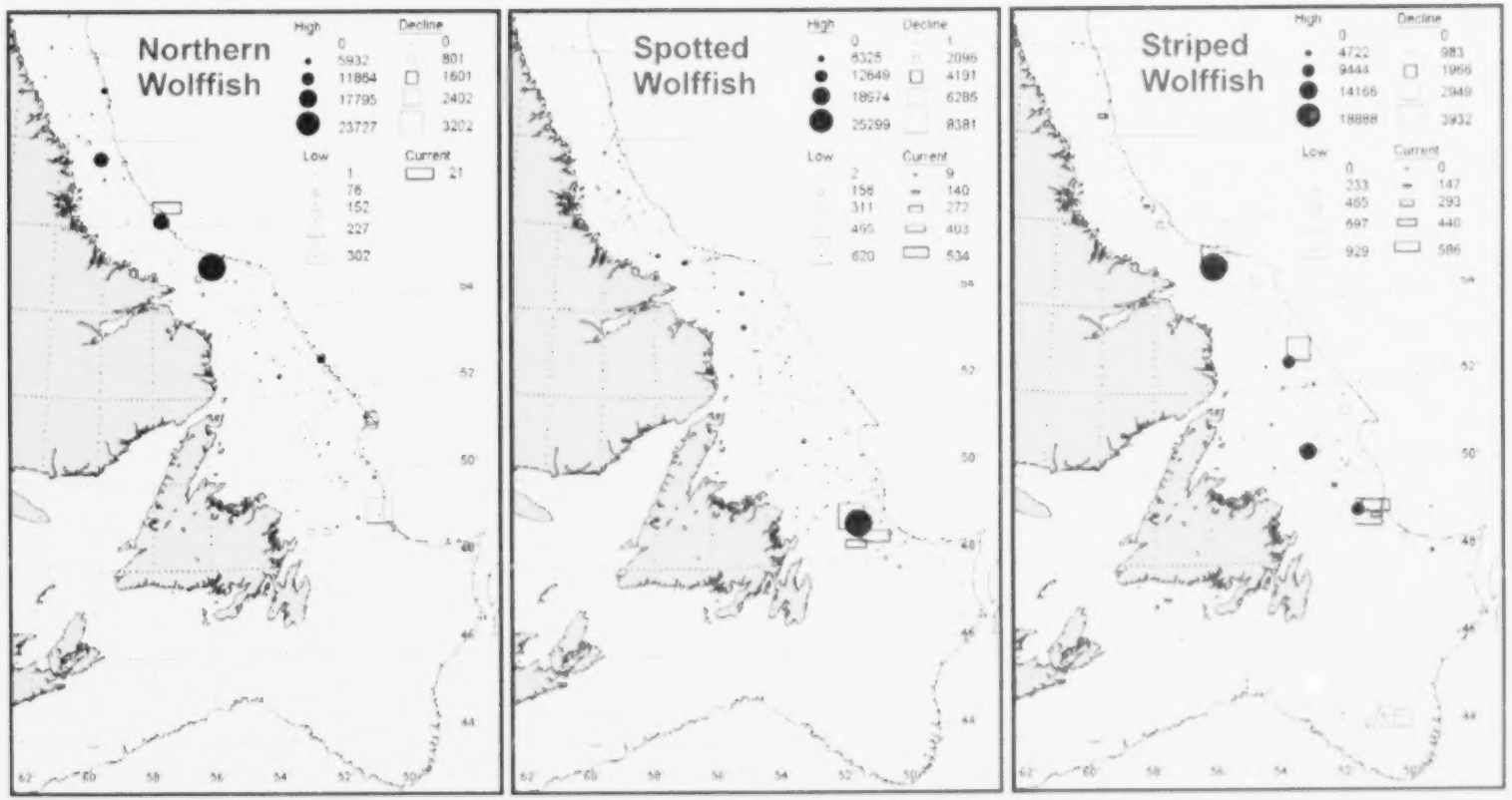

Figure 6. Location of high density centroids. Each centroid geo-references the center of the highest concentrations of fish (refer to the highest category on the legends of Fig. 2). Size of symbol denotes area of the high concentration.

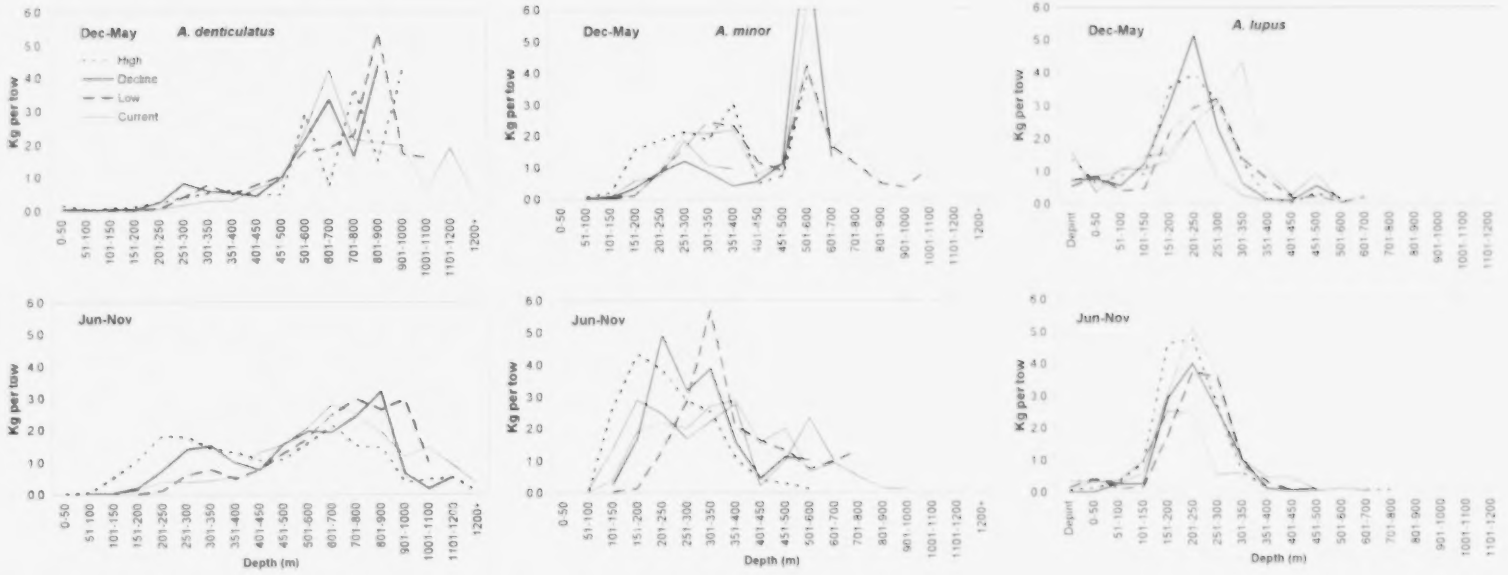

Figure 7. Distribution of wolffish in relation to depth. Periods: High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003. Data are standardized kg/tow from NL research surveys.

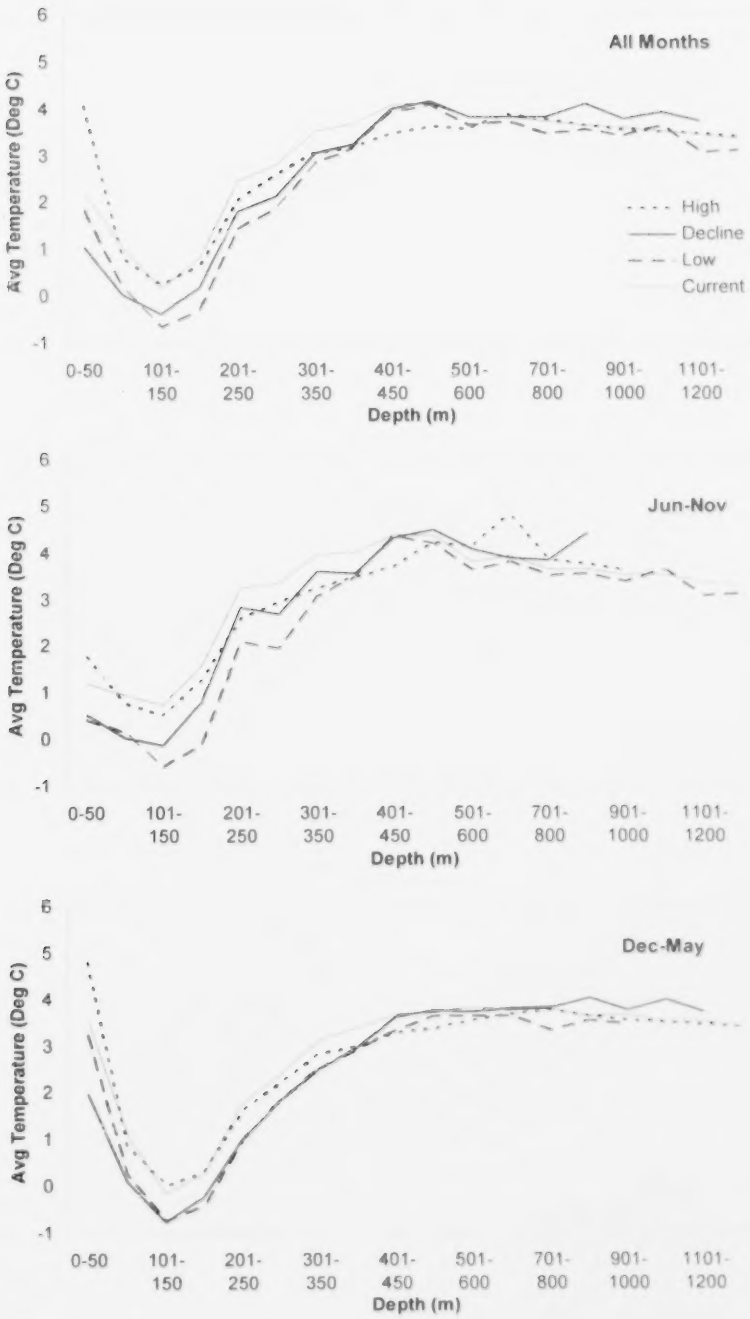

Figure 8. Average temperature within depth intervals. Periods: High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003.

Figure 9. Spatial extent of bottom temperature expressed as percent of total area associated with temperature ranges by period (High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003).

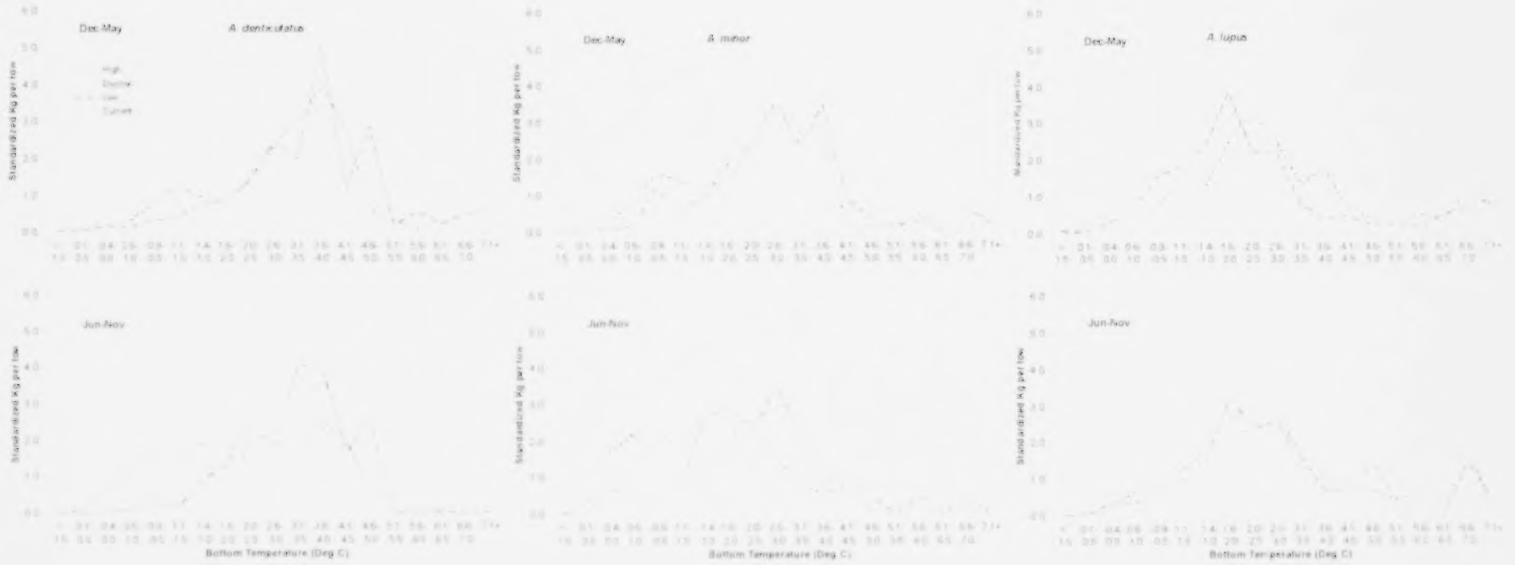

Figure 10. Distribution of wolffish in relation to bottom temperature. Periods: High, 1978-1984; Decline, 1985-1989; Low, 1990-1995; 1995-2003. Data are standardized kg/tow from NL research surveys.

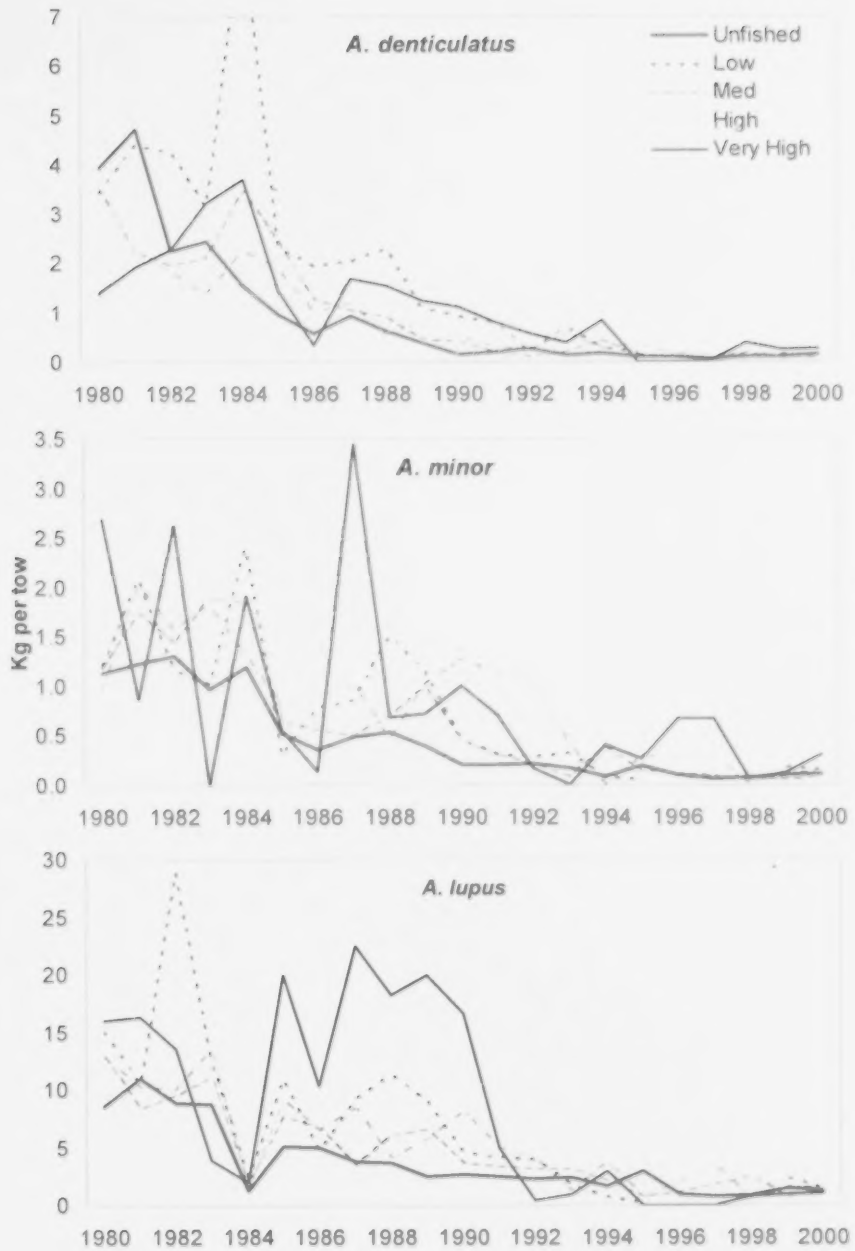

Figure 11. Annual changes in density (standardized kg per tow) of wolffish species with respect to intensity of trawl fishing effort (trawl data from Kulka and Pitcher 2001).

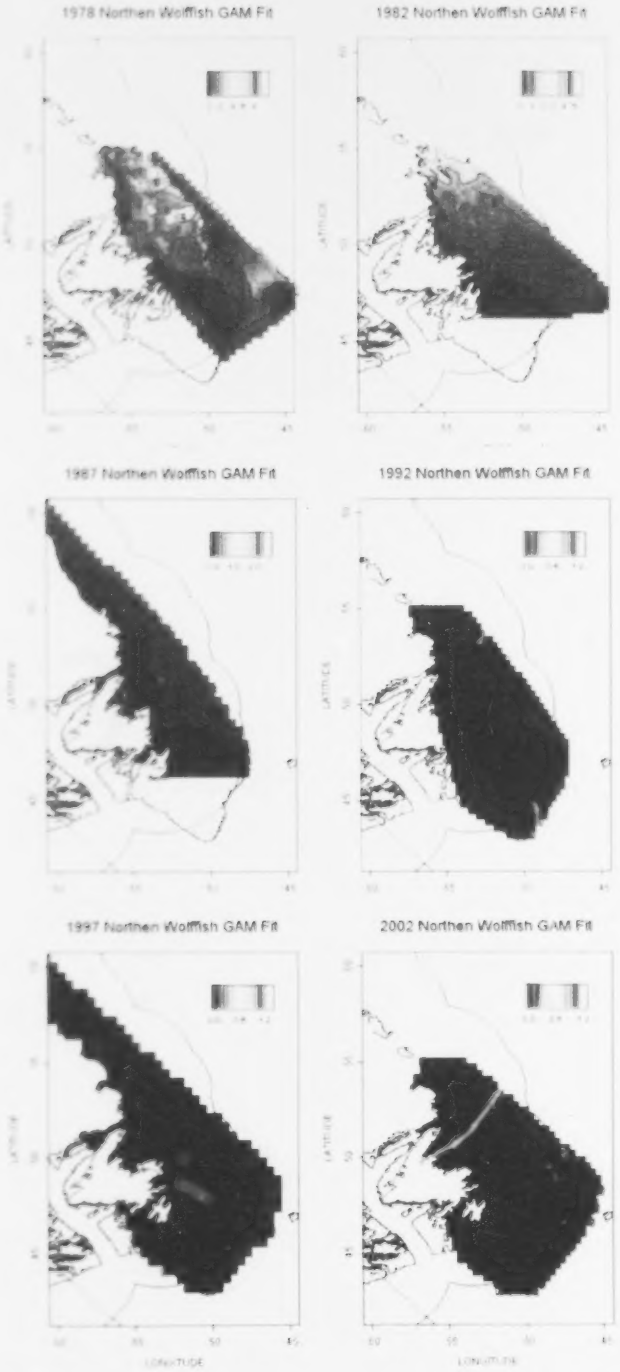
1978 Northen Wolffish GAM Fit
1982 Northen Wolffish GAM Fit
1987 Northen Wolffish GAM Fit
1992 Northen Wolffish GAM Fit
1997 Northen Wolffish GAM Fit
2002 Northen Wolffish GAM Fit

Figure 12. Distribution of *A. denticulatus* abundance based on the generalized additive model fit in select years from research surveys. Blue represents areas surveyed but no catch. Orange represents high catch rates.

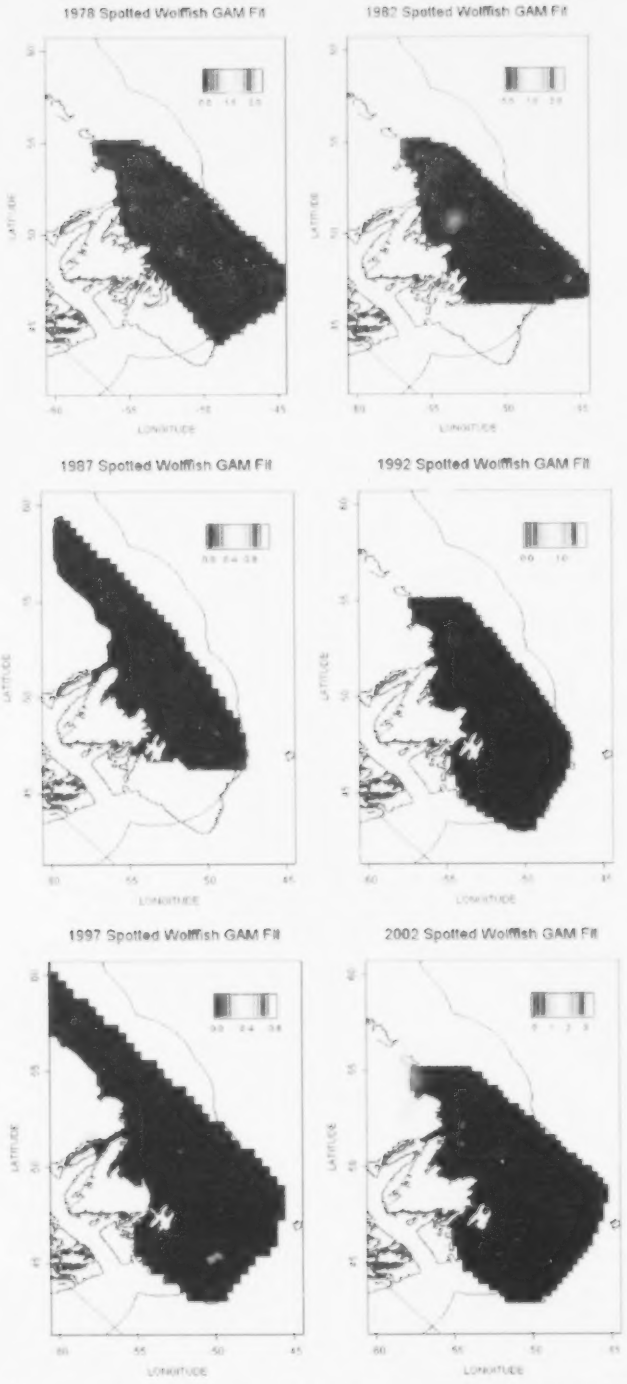
1978 Spotted Wolffish GAM Fit
1982 Spotted Wolffish GAM Fit
1987 Spotted Wolffish GAM Fit
1992 Spotted Wolffish GAM Fit
1997 Spotted Wolffish GAM Fit
2002 Spotted Wolffish GAM Fit
LATITUDE
LONGITUDE

Figure 13. Distribution of *A. minor* abundance based on the generalized additive model fit in select years from research surveys. Blue represents areas surveyed but no catch. Orange represents high catch rates.

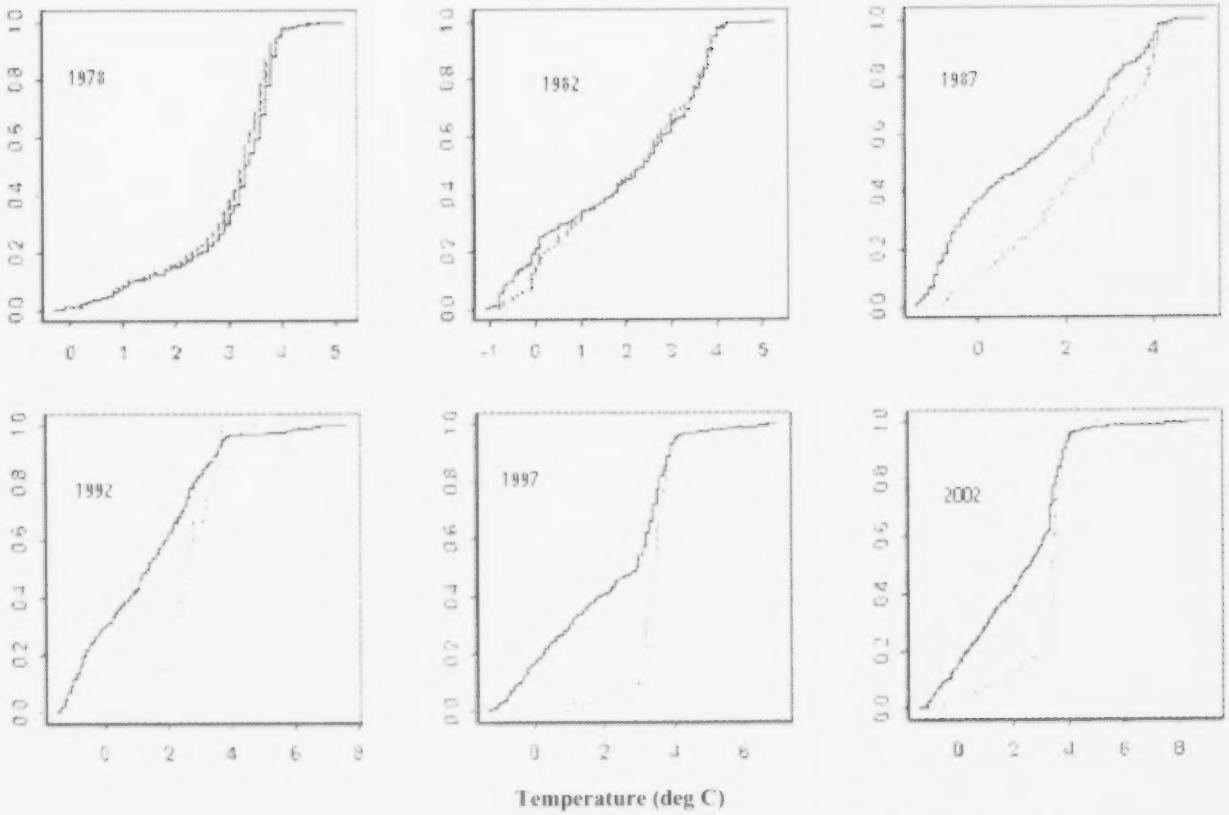

Figure 14. Bottom temperature probability distribution plots for all survey sets available in select years (solid) and capture locations of *A. denticulatus* (dashed lines). Cumulative distribution on Y axis.

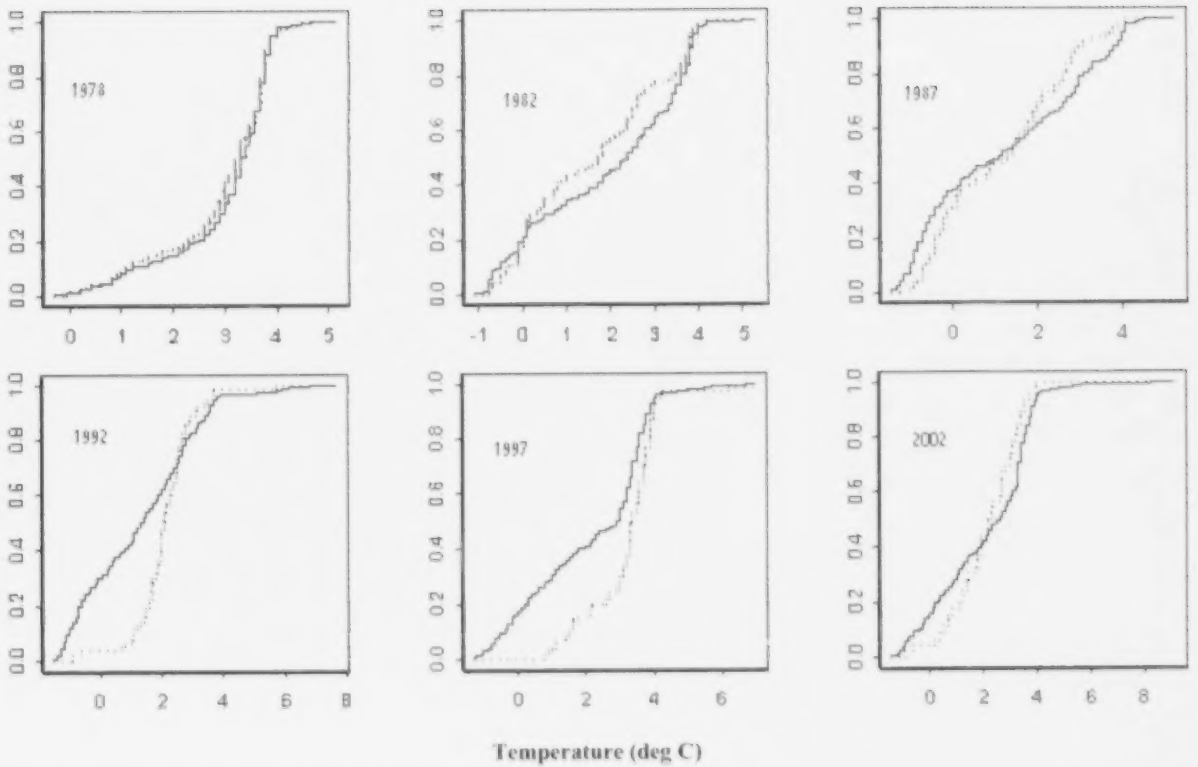

Figure 15. Bottom temperature probability distribution plots for all survey sets available in select years (solid) and capture locations of *A. minor* (dashed lines). Cumulative distribution on Y axis.

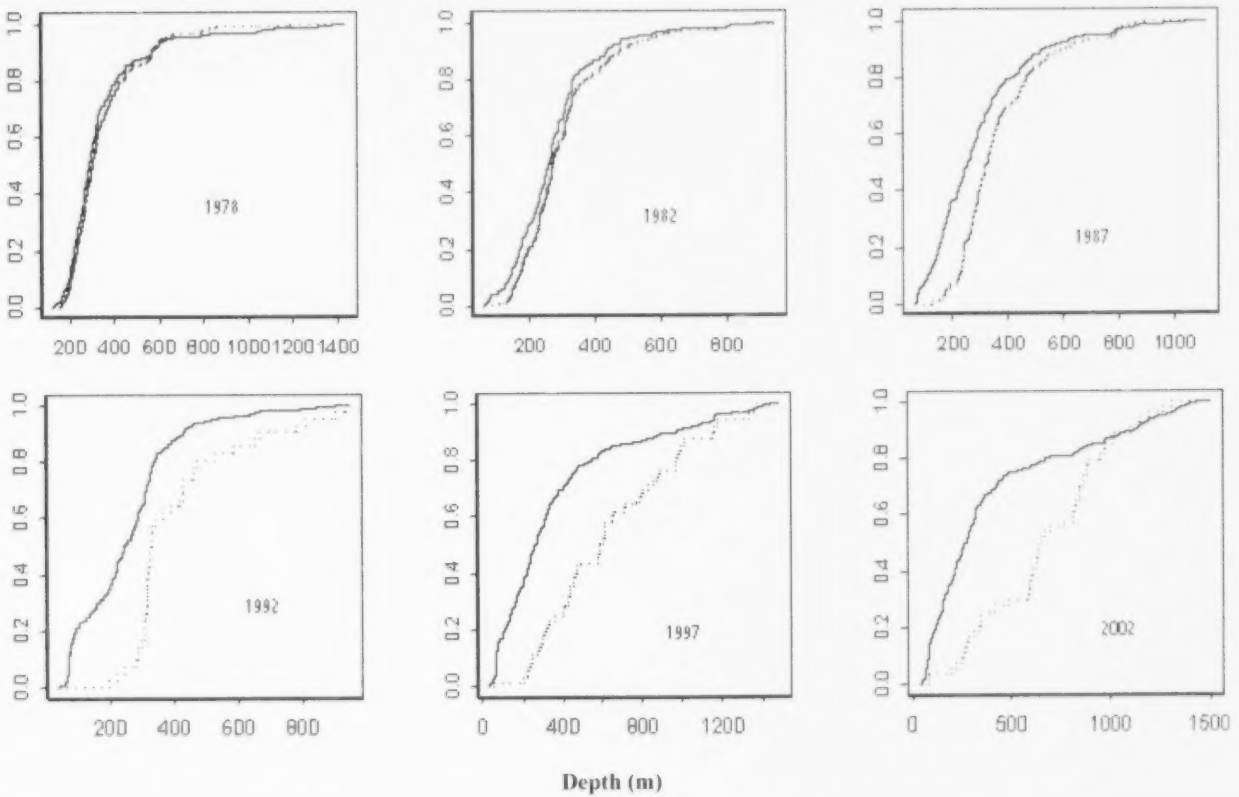

Figure 16. Bottom depth probability distribution plots for all survey sets available in select years (solid) and capture locations of *A. denticulatus* (dashed lines). Cumulative distribution on Y axis.

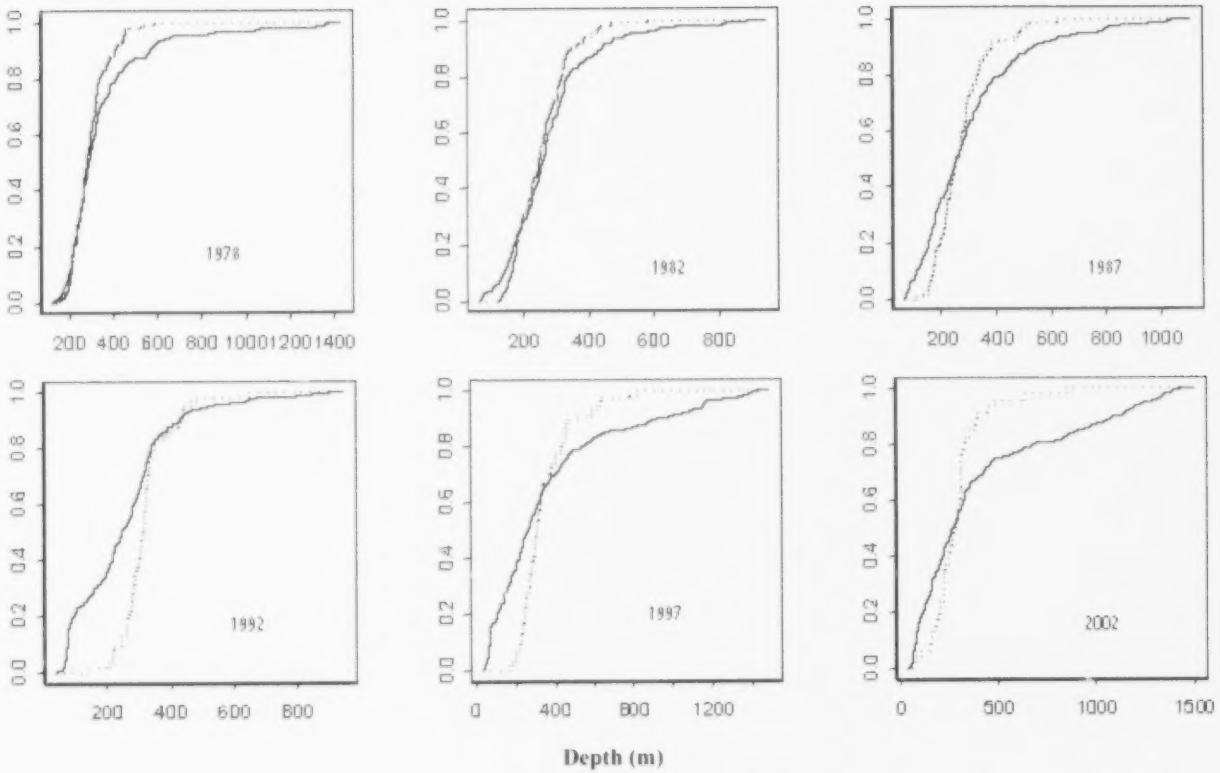

Figure 17. Depth probability distribution plots for all survey sets available in select years (solid) and capture locations of *A. minor*.(dashed lines). Cumulative distribution on Y axis.

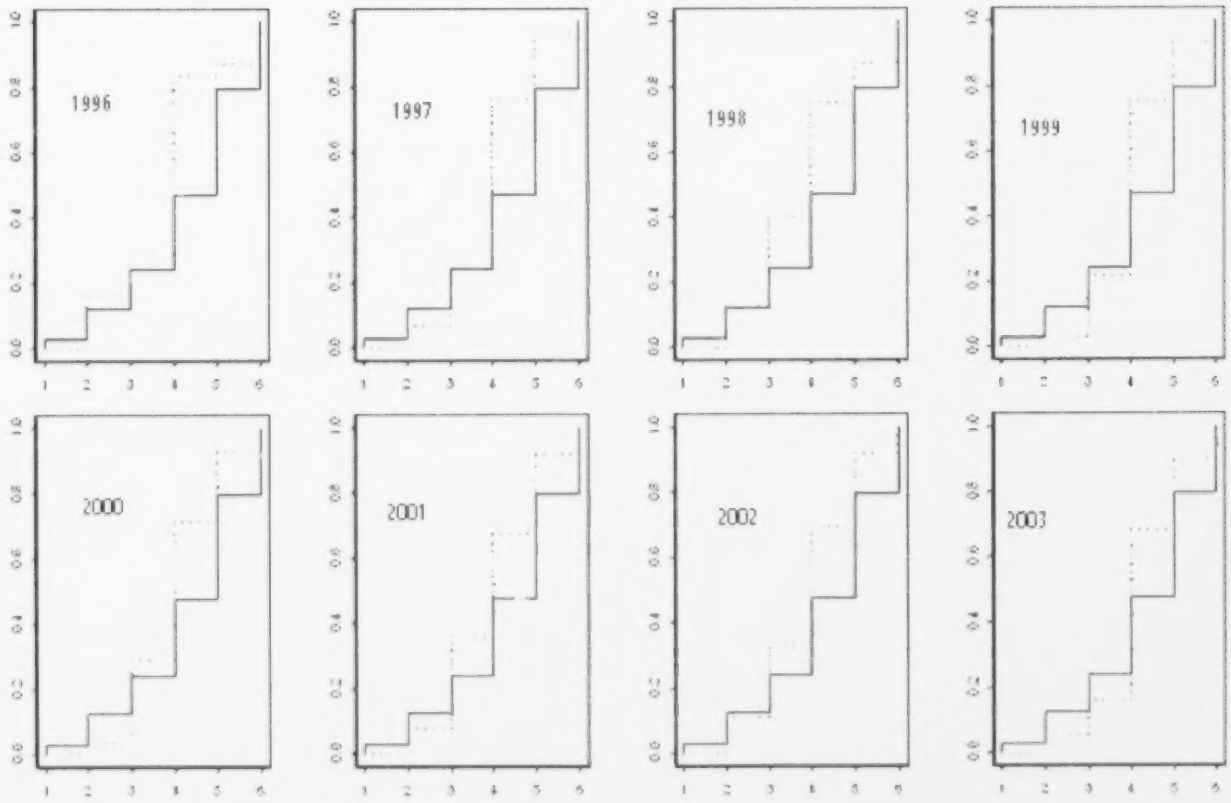

Figure 18. Sediment type probability distribution plots for all survey sets available in select years (solid) and capture locations of *A. denticulatus* (dashed lines). Cumulative distribution on Y axis. Refer to Table 4 for sediment types.

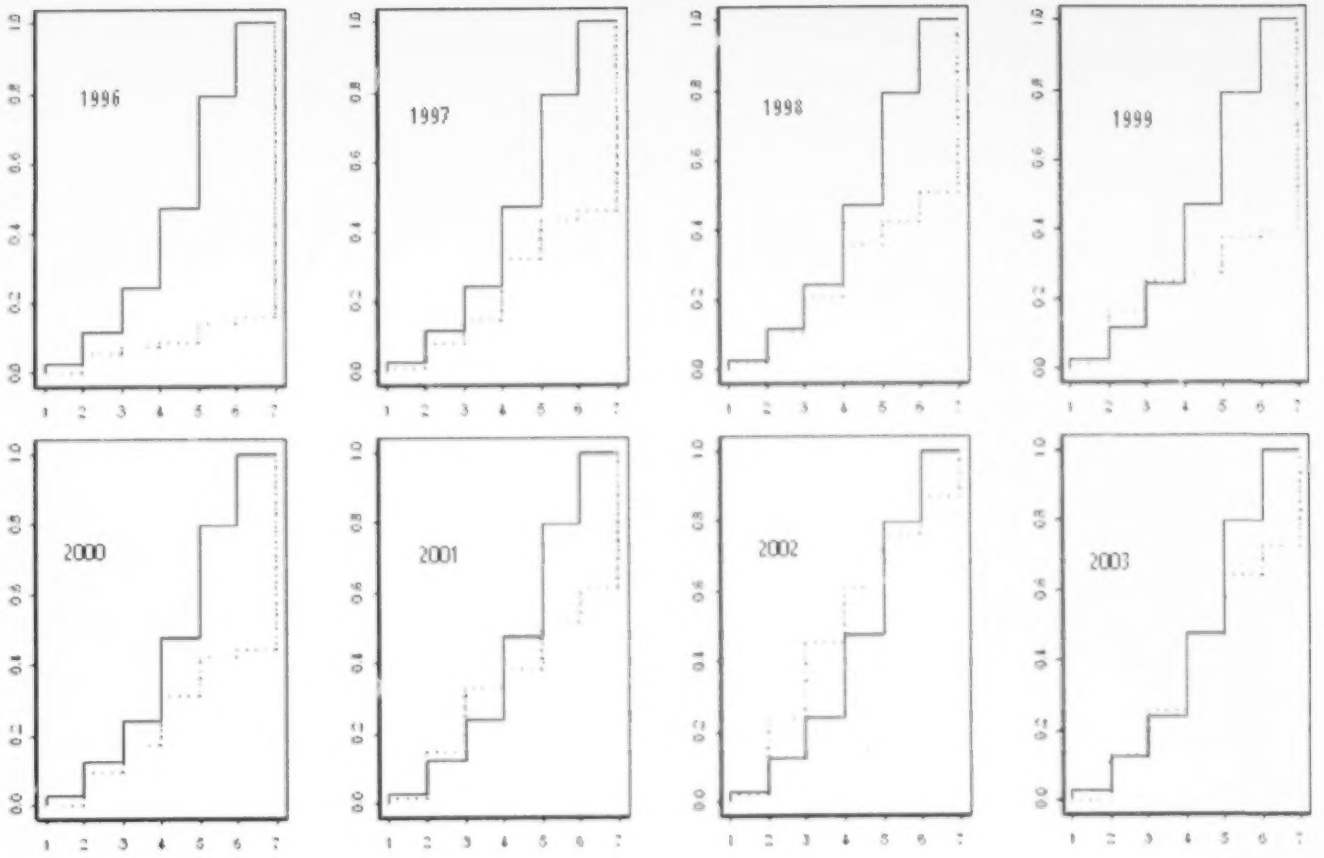

Figure 19. Sediment type probability distribution plots for all survey sets available in select years (solid) and capture locations of *A. minor* (dashed lines). Cumulative distribution on Y axis. Refer to Table 4 for sediment types.